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# Effects of food limitation on social grouping and foraging in a fission-fusion species

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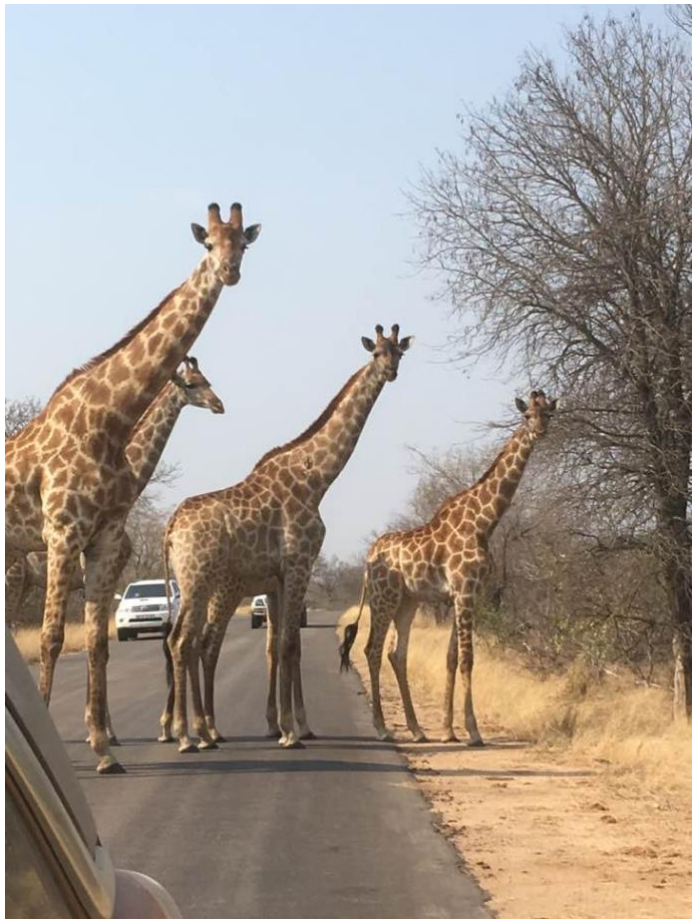

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# Abstract

Social groups form when the benefits of group association outweigh the costs. In fission-fusion societies, groups change in response to current local conditions rather than being fixed as seen in stable groups. This flexibility allows individuals to counterbalance the negative consequences of grouping by splitting into small groups but then aggregate again when it is beneficial. The composition may also be in constant flux, resulting in changing group composition and, sometimes, sexual segregation. Furthermore, individuals form associations within groups, such that social costs and benefits may be experiences not only in relationship to group size or composition but by the identity of a close neighbour, which could be a better representation of social effects within a group. Harassment by males, usually related to mating, is a one common behaviour that had a negative influence on individuals and causes changes to behaviour, which could be altered by group composition or near neighbour.

Male harassment occurs in giraffe due to their polygynous and asynchronous breeding, and they exhibit fission-fusion groups, so that they can respond to costs and benefits of grouping. They also show a degree of sexual segregation throughout the year. Furthermore, due to their large body size, they require a large amount of food, and may be particularly sensitive to food limitation. In addition, giraffe are currently undergoing what has been termed a 'silent extinction', with numbers from falling 155 000 to 97 000 over 30 years. Up until recently there has been little research conducted on giraffe, therefore, we need a better understanding of their ecology and behaviour to be able to stem the loss in numbers and develop more effective management plans for the conservation of the species. It is important to know more about environmental variability, especially with common events like drought, so we can improve management responses to such events.

In this thesis I tested if giraffe females change their foraging behaviour in relation to their immediate social group and their nearest neighbours. I found that female giraffe change their foraging efficiency if a large male is present, therefore there is a foraging cost to being

near large males. My research shows that giraffe are influenced by their close neighbours and this may influence their behaviour more than group composition as a whole. I found that seasonal variation alters these behavioural patterns. I also test if foraging behaviour is changed with food availability. After periods of drought there is less food available and female giraffe become more tolerant to the presence of male close neighbours as there are fewer foraging options. I test if there is sexual segregation in giraffe populations and found the degree of segregation changes with environmental and food availably differences. I tested a range of sexual segregation hypotheses and found that sexual segregation is caused by a combination of different factors including social influences and by physical differences caused by distinct sexual dimorphism in giraffe.

Food limitation effects social interactions in giraffe populations and knowledge of environmental conditions that can alter food availability is important for conservation efforts for this species. By looking at close neighbour effects in a fission-fusion species we can better understand the costs and benefits of grouping and how these groups are formed and maintained.

# Chapter 1: General Introduction

Social grouping and social relationships influence most aspects of ecology but until recently research has been largely confined to studies addressing questions in behavioural ecology. Social relationships can, however, influence species conservation outcomes, which is being increasingly recognised (Anthony & Blumstein, 2000; Berger-Tal & Saltz, 2014; Renan et al., 2018). Relationships form the basis of social groupings and impact every aspect of an animal's life, altering foraging success, habitat choice, mate selection and ultimately reproduction and survival (Majolo et al., 2018). While social relationships influence ecology, ecological factors, such as predation and the distribution of resource also play a crucial role in shaping social structures (VanderWaal et al., 2014).

In mammals, the formation of groups can be beneficial for individuals because it provides greater protection from predators, improves success in locating or maintaining access to resources and creates mating opportunities (Clutton-Brock, 2016), as well as other additional fitness benefits (reviewed in Silk, 2007). However, grouping can also be costly for individuals because it can increase competition for resources and mating opportunities, exposes individuals to higher risks of infection and disease, and can attract predators (Silk, 2007; Clutton-Brock, 2016). Therefore groups are most likely to occur when the net benefits of being in a group are greater than the costs that come from living in close proximity to conspecifics (Silk, 2014).

Reproductive success can be increased by having close social relationships. In cooperative breeding house mice (*Mus domesticus*), for example there was higher reproductive success for the females that had closer relationships with their social partner (Weidt et al., 2008). Similar fitness and reproductive success benefits are seen in dolphins (*Tursiops* sp.) (Frère et al., 2010), horses (*Equus ferus caballus*) (Cameron et al., 2009) and baboons (*Papio cynocephalus*) (Silk et al., 2003). Other fitness benefits that can occur include helping to protect from infanticide (Palombit et al., 1997) and improved longevity in baboons (Silk et al., 2010). Close social relationships can also reduce harassment in horse groups (Linklater et al., 1999) and promote the reduction of stress in female baboons (Wittig et al., 2008). When eastern grey kangaroos (*Macropus giganteus*) were grazing with other kangaroos with whom they frequently associated, they spent less time on vigilance behaviour and

more time foraging (Carter et al., 2009). This would provide an increase in fitness as they would be able to have a higher food consumption. Time spent with closer individuals, may improve their feeling of security and potentially make them more confident in their pairs to warn them of any danger. Thus, social relationships within a group provide multiple benefits.

Being social can also have negative impacts on an animal's individual fitness. Group-living increases competition for resources or mates and can increase spread of diseases and make animals more conspicuous to predators (Silk, 2007). Group living also increases interactions with conspecifics including negative behavioural exchanges, such as male harassment. Harassment effects can scale up to have impacts of grouping and social structure of group-living animals. In animals as taxonomically diverse as horses and guppies (*Poecilia reticulata),* harassment influences interactions between females (Linklater et al. 1999; Cameron et al., 2009; Darden & Watts, 2012) including the formation of stable relationships between females to reduce the harassment (Cameron et al., 2009). This results in differences in group dynamics; in mosquito fish (*Gambusia holbrooki*) females harassed by a male spent more time near larger groups of other females to dilute male disturbance and would also approach other males while being harassed to promote male-male interactions (Agrillo et al., 2006). It can drive female guppies into new habitats, that they would normally not prefer, but where there are fewer males (Darden & Croft, 2008).

Social interactions can form the basis of the structure within a group. In group living mammals, the ability to build a stable social system is thought to rely on the ability of individuals to establish and respect dominance relationships (Sachser et al., 1998). Forming bonds with an individual who is higher up the hierarchy can improve the lower ranking individual's status in the hierarchy and they will receive addition benefits that come with being a more dominant individual, for example, priority and increased access to resources. Consequently, relationships within a group can mitigate some of the costs of grouping (Cameron et al. 2009) thereby enhancing the benefits.

A full understanding of the costs and benefits of grouping therefore requires an understanding of grouping patterns and within group relationships. Animals can be solitary in nature and generally only come together for breeding events and this is seen in many carnivore species, for example a leopard (*Panthera pardus*) (Sandell, 1989). Animals can live in a monogamous pair bond relationship, where a male and female of the species will live together and raise young (Poole, 1985). Young will usually disperse once they have matured. In these relatively solitary species, the costs of grouping generally outweigh the benefits.
In more social species, there are a variety of structures. Family groups occur when all family members live together in a group, with young remaining with the family until fully grown (Poole, 1985). Pack like structures provide benefits of easier hunting, for example with African wild dogs (*Lycaon pictus*) (Carnaby, 2006). A herd structure is common in ungulate species where there is usually one dominant male and many females (Rowell, 1987). Some are permanent like the zebra (*Equus burchellii*) (Fischhoff et al., 2007), while others will only be formed in the breeding season and will dissolve shortly after like impala (*Aepyceros melampus*) (Carnaby, 2006). Multi-sex groups also exist, where adults of both sexes live together in a permanent group (Poole, 1985). These groups can be a matriarchal group of related females, which is a group of bonded females and those female's young and grown daughters (Poole, 1985), such as elephants (*Loxodonta africana*) (Carnaby, 2006). An oligarchy group is a complex system which is ultimately run by an 'elite gang of dominant males' (Carnaby, 2006), such as in Chacma baboons (*Papio ursinus)* (Carnaby, 2006). A pride of lions (*Panthera leo*) is another example of a multi sex group, with males and females that are usually related are living together, providing benefits with hunting and raising cubs (Poole, 1985). All of these groups remain relatively consistent across time. A fission-fusion social structure is where members of the group form temporary associations, with individuals leaving and joining the group with no permanent relationships (Dagg, 2014), such as kangaroos (Best et al., 2013) and orangutans (*Pongo pygmaeus*) (van Schaik, 1999). These are of particular interest since the groups change in response to current conditions, providing insight into costs and benefits of grouping. These aspects of fission-fusion groups are under studied and have the potential to expand our knowledge on how groups are formed and what causes them to break up.

## *Fission-fusion groups*

Fission-fusion groups are flexible joining together and splitting up regularly (Couzin, 2006). This structure can be found in a variety of different species such as modern day humans (*Homo sapiens*) (Aureli et al., 2008), chimpanzees (*Pan troglodytes verus*) (Lehmann & Boesch, 2004), dolphins (Smith et al., 2016) and even species of bats (*Nyctalus lasiopterus*) (Popa-Lisseanu et al., 2008). Fission-fusion dynamics were thought to only be exhibited in animals with higher cognitive capacity, such as dolphins and chimpanzees (Aureli et al., 2008) but this social structure is also found in species with passive 'self-sorting', the most basic form of fission-fusion, e.g. guppies (Couzin, 2006; Croft et al., 2004). There are also animals that exhibit an 'active' preference of association, and often associating with more familiar individuals (Couzin, 2006), such as giraffe (*Giraffa camelopardalis*) (Carter et al., 2013b). Fission-fusion groups likely evolved as an adaptive strategy to the unpredictable distribution of resources, where food sources may not always accommodate all animals within the group, so fission reduces competition between individuals (Majolo et al., 2018). These dynamics are therefore a product of ecological variation (Webber & Vander Wal, 2018). The fluidity of fission–fusion social systems allows animals to counterbalance negative consequences of grouping by splitting in small groups but then aggregate again when it is beneficial (Popa-Lisseanu et al., 2008). This flexibility of restructuring into subgroups enables a response to changing environmental conditions (Popa-Lisseanu et al., 2008). This enables the exploration of fission or fusion events and the resulting groups and test the drivers of these events, and the related costs and benefits to the individual for making those decisions.

## *Foraging*

Social behaviours can influence essential activities, including foraging. The fitness of a foraging animal is a function of the efficiency of its foraging (Pellew, 1984). Therefore, any behaviour that may influence foraging efficiency is important to understand to help maintain that animal's fitness and overall survival. It is also important to help in wildlife management and to know that animal's role in the ecosystem (Mahenya, 2017). Larger

individuals will require more absolute food than smaller individuals (du Toit & Yetman, 2005), but lower mass-specific requirements, which forms the basis of the Jarman-Bell principle (Bell, 1986, 1971). This states that an increase in ungulate body size is associated with an increase in dietary tolerance and can predict the ecological roles of species. Foraging efficiency is affected by forage availability, itself influenced by environmental events such as droughts (Vetter, 2009). This changes the food availability and therefore foraging behaviour for the animals in that area. When food becomes scarce in southern Africa, elephants tend to knock down trees to be able to access the tops of trees to get more food (Bax & Sheldrick, 1963), further altering the food availability and the composition of the vegetation. Therefore, food availability can influence an individual's health and survival and this could alter their behaviour and interactions.

## *Sexual Segregation*

Sexual segregation is where male and females of a species live in separate groups outside of breeding season, sometimes using different home ranges and type of habitat, and is found in a variety of different species (Ruckstuhl, 2007). Dimorphism in body size can also lead to sexual differences in ecology and behaviour, making it difficult for the two sexes to stay in the same group (Ruckstuhl, 2007). Sexual segregation is common in many ungulate species, such as bighorn sheep (*Ovis canadensis*) (Ruckstuhl, 1998) and some marsupials, such as the western grey kangaroo (MacFarlane & Coulson, 2007). Sexual segregation indicates that there are dynamic groups, like fission-fusion, which respond to social and/or environmental factors (reviewed in Ruckstuhl 2007).

Social interactions could be a means by which sexual segregation is created and maintained. The social preferences hypothesis suggests that the differences in behaviour between the sexes is what causes the differing habitat use (Bon & Campan, 1996). Male harassment may influence segregation (Darden & Croft, 2008), since this aggressive male behaviour could drive females away from the males to avoid this behaviour (Bon et al., 2001). It is thought that this causes sexual segregation in elephants, when females move away to try and avoid unwanted sexual behaviour and aggression from males but also for males to avoid

aggressive behaviour from females (Siyaya, 2015). A fission-fusion social structure allows individuals to be able to avoid and move away from aggressive and costly behaviours from other individuals within environmental constraints (Darden & Watts, 2012). Such segregation may also be affected by the social interactions between individuals and vary with food availability and season. Fission-fusion systems again provide the ideal opportunity to be able to test these hypotheses, as we can observe fission/segregation events and the interactions or behaviours that initiated the separation.

## *Environmental Conditions*

Droughts are a frequent occurrence in South Africa (Vetter, 2009) and have the potential to radically alter the vegetation type and cover in a particular area. The impact of drought on natural ecosystems is mostly on plant cover and biomass production (Le Houérou, 1996). Some droughts may only be short-term and then followed by recovery during subsequent years of higher rainfall, but in some cases droughts can trigger substantial and sometimes irreversible ecological changes (Vetter, 2009). A common result of extreme drought is that of desertification, the process of land degradation that reduces its productivity (Nicholson et al., 1998). Habitats that were previously dominated by woody vegetation can, post drought, become a more open grassland (E. Cameron, personal communication, September 2017). This change is aided in part by elephants knocking down trees at greater rates in times of drought (Bax & Sheldrick, 1963). Such ecological changes will therefore also change the food availability in a region, especially for browsing species. The increased pressure of climate change means that extreme weather events like drought will become more prevalent and widespread (Watson & Albritton, 2001), therefore knowing what the consequences are and how to recover from them becomes even more important.

## *Giraffe*

The social structure of giraffe herds is a fission-fusion society (Dagg, 2014). This structure occurs when members of the group form temporary associations, with members coming and going from groups with no apparent bonds or relationships (Dagg, 2014). It is now

believed that the social relationships may be more complex since there is evidence of social bonds formed between females in captive populations (Bashaw et al., 2007) and case of separation anxiety when individuals have been removed (Tarou et al., 2000). Research in the field has found that some giraffe females had long-term relationships that had spanned over 6 years (Carter et al., 2013a). So although giraffe social interactions are highly fluid in nature, there are apparent association patterns in giraffe that are not the result of random fission–fusion events, but are embedded within a structured social network characterised by multiple levels of organization (VanderWaal et al., 2014). The presence of other giraffes within a group could therefore affect a giraffe's behaviour more than previously thought. Giraffe also exhibit distinct sexual segregation in populations, both on a horizontal habitat scale by groups and a vertical scale in terms of foraging heights (Ginnett & Demment, 1999).

Recently it has been proposed that giraffe are able to communicate over larger distances via infrasound (Bashaw, 2003; Dagg, 2014). Infrasound is vocalisations that are made at a frequency of less than 20 Hz and are too low for humans to hear (Pye & Langbauer Jr, 1998). So while giraffe herds share many characteristics of fission–fusion social systems, their communication systems may be a crucial component regulating subgroup dynamics (Bercovitch & Berry, 2013). However more research is required to fully determine how giraffe do communicate over distances and between groups (Kasozi & Montgomery, 2018).

Human observers may lack the ability to measure a group as perceived by a giraffe, as what we consider to be a group may have little relevance to a giraffe (Cameron & du Toit, 2005), which may have contributed to the perception that giraffe were asocial. The use of infrasound and olfactory cues and their greater distance of vision may enable cohesion in a group, over a large dispersed wide ranging area but in relatively stable social groups not easily detectable by observers (Doherty, 2005). Studies on social networks suggest a social organisation that we don't fully understand. Near neighbours may be more important than the group size itself when it comes to social effects on individuals (Rolando et al., 2001). Therefore nearest neighbour or proximity measures may be better suited to describe social preferences (Bashaw et al., 2007). Consequently, both the group and close spatial relationships likely provide benefits to other aspects of their ecology such as foraging

behaviours. If males harass it would be beneficial for a female to avoid spending time around males and instead group with other females.

Giraffe show a high degree of sexual dimorphism (one of the highest of all land mammals), in both height and weight. Male giraffe weigh approximately 1200kg and female giraffe weigh approximately 800kg (Dagg & Foster, 1976). Males are also taller than females, with males ranging from 4.7m to 5.3m and females ranging from 3.9m to 4.5m (du Toit, 2001). This dimorphism can be a cause of sexual segregation in giraffe populations due to differences in foraging requirements as well as social preferences.

As giraffe are very large ruminants they have to spend a large amount of time feeding to meet daily intake requirements (du Toit & Yetman, 2005). Seasonal shifts in availability of food and local rainfall have been reported to increase giraffe herd sizes (Fennessy, 2004). Consequently, giraffe may be less concerned about conspecifics then they were previously due to the lower food availability. Giraffe are considered to be 'exclusive browsers', feeding on plants and shrubs 2-5m above the ground (Seeber et al., 2012), however they can very occasionally graze on grass. When doing this they must use the same splayed leg posture they adopt for drinking (Seeber, et al., 2012). This position means they are particularly vulnerable to attack from predators (Périquet et al., 2010). The frequency of grazing may increase but this would also increase predation risk. It can also reduce the opportunity for vertical sexual segregation in foraging height, although interspecific competition still exists at lower heights for species such as kudu (*Tragelaphus strepsiceros*) so may mean that males will still forage higher as they are the only ones who can reach that height. It may then mean that as browsing resources become scarcer, female giraffe will increase their tolerance to male conspecifics.

## *Rationale*

Giraffe are currently undergoing what has been termed a 'silent extinction,' with numbers dropping from 155,000 in 1985, to just 97,000 in 2015 (Muller et al., 2016) and they have recently been listed on the red list for the first time. Giraffe were not considered to be at

risk of reaching threatened status as they are a conspicuous mega-fauna. Furthermore, there is a current debate about whether giraffe are one species with different sub-species or whether there are four distinct species (Bercovitch et al., 2017; Winter et al., 2018); further complicating the conservation discussion as this would make some species critically endangered. Up until recently there are been few field studies that have focused on giraffe (Bercovitch & Deacon, 2015). It has been identified as recently as last year that further research is necessary to understand the complex behaviour and ecology of this prominent yet understudied species (Muller et al., 2018). This means that there is a lack of knowledge of these charismatic animals. It is important for us to have a better understanding of the ecology and behaviours of this species so that we can help to stem the number of individuals being lost (Mahenya, 2017), and develop more effective conservation strategies to help giraffe management in the wild as well as in captivity by improving species management plans (Seeber et al., 2012). Since we are only beginning to understand their social grouping and its impact on ecology, this is an important area of research, particularly in relation to environmental pressures.

A species can decline due to a variety of different factors. Disease has the ability to wipe out entire populations. Animal population substructure has profound implications for the transmission of disease (Couzin, 2006). It is important to know how individuals interact with each other in case of an outbreak of an infectious disease, and thus helping to contain its spread and combat it effectively (Dagg, 2014). In a reintroduced population, the social behaviour of the species can strongly affect the long-term viability of the population through its effects on movement, information flow, disease spread and the population's genetic variability (Renan et al., 2018). Therefore, information on the social behaviour of a reintroduced population can contribute to conservation practices; however, its importance is often underestimated (Renan et al., 2018).

With a declining population, the mating potential for individuals within that population will decrease. It becomes harder to find potential mates and ensure a successful mating. Subsequently there will be a decrease in genetic variability (Renan et al., 2018), as the number of individuals available to mate with decreases, this will limit the number of new

genes entering a population. With less genetic diversity the population is more at risk of not being able to combat such things as disease and environmental changes.

With the increase of drought that is predicted to occur due to climate change (Watson & Albritton, 2001), animals will increasing face periods of decreased food availability. This will increase competition between individuals and may result in more animal deaths (Mitchell et al., 2010). Larger males become at risk as they can no longer meet their high demand for the amount of food they require, as well as juveniles as they are unable to compete as well for resources (Mitchell et al., 2010). The number of individuals supported in an area may be reduced with the increased drought risk. This makes the knowledge of conditions important to know to be able to maintain a healthy population and be able to make informed decisions about translocations.

This research aims to help provide better knowledge of giraffe social behaviour by determining the effects of close neighbours in a fission-fusion species and the factors that may influence fission and fusion events. I will test social influences on foraging behaviour, including environmental variability. It is important as droughts are a common occurrence in South Africa (Vetter, 2009), and by understanding how they change the behaviour of individuals it can help species management in the wake of such events. I also aim to test different hypotheses of sexual segregation in a giraffe population.

## *Hypotheses*

1) Female giraffe will avoid feeding near mature bulls to avoid harassment, increased vigilance and foraging loss.

2) After a period of drought (2015/2016) and while the vegetation recovers, females will be less able to avoid males and therefore will feed closer to them than pre-drought due to reductions in foraging options, which is predicted to reduce foraging efficiency.

3) Sexual segregation on a horizontal scale will be less pronounced as the decrease in food availability will cause all individuals to have to forage in closer proximity.

## *Study Site*

Research was undertaken in Kruger National Park (KNP) in the North-East region of South Africa. It covers an area of 19,485 km² and is one of the largest reserves in Africa. It has many different ecotypes such as open savanna, bushveld and mixed woodlands. This diversity in habitat allows it to host a large array of animals including the 'Big 5'; lions, leopard, rhino, elephant and buffalo. KNP is home to approximately 8300 giraffe (South African National Parks – SANParks – Official website). The region has distinct wet and dry season, with the rainy season beginning in October/November and continuing until May. The dry season then commences from May until October again. Food becomes plentiful with the commencement of the rain but starts to become scarce around the middle of the dry period. This creates a seasonal variation in food supply. Data for this project was collected around the Tshokwane region of the park (Figure 1.1, circled), with Satara rest camp designating the upper limit and Lower Sabie rest camp being the lower limit of the collection region.

KNP suffered a large flood event in 2000, after which food become plentiful (Figure 1.2). KNP has since undergone a sustained period of drought over a two-year period from 2014 until 2016. According to the official KNP (SANPark) website, the wet season of 2014/2015 saw only 255mm fall which is only 65% of the yearly average. It became even worse the following year with the 2015/2016 season only having 190mm rain as opposed to the normal 550mm (52% of the normal average). 2016/2017 season saw an increase in rainfall with 371mm falling. The 2018 dry season has been particularly hot again with the onset of the rainy season not starting until November, a month later than normal. This drought has dramatically changed the vegetation cover and food availability in the park (Figure 1.3).

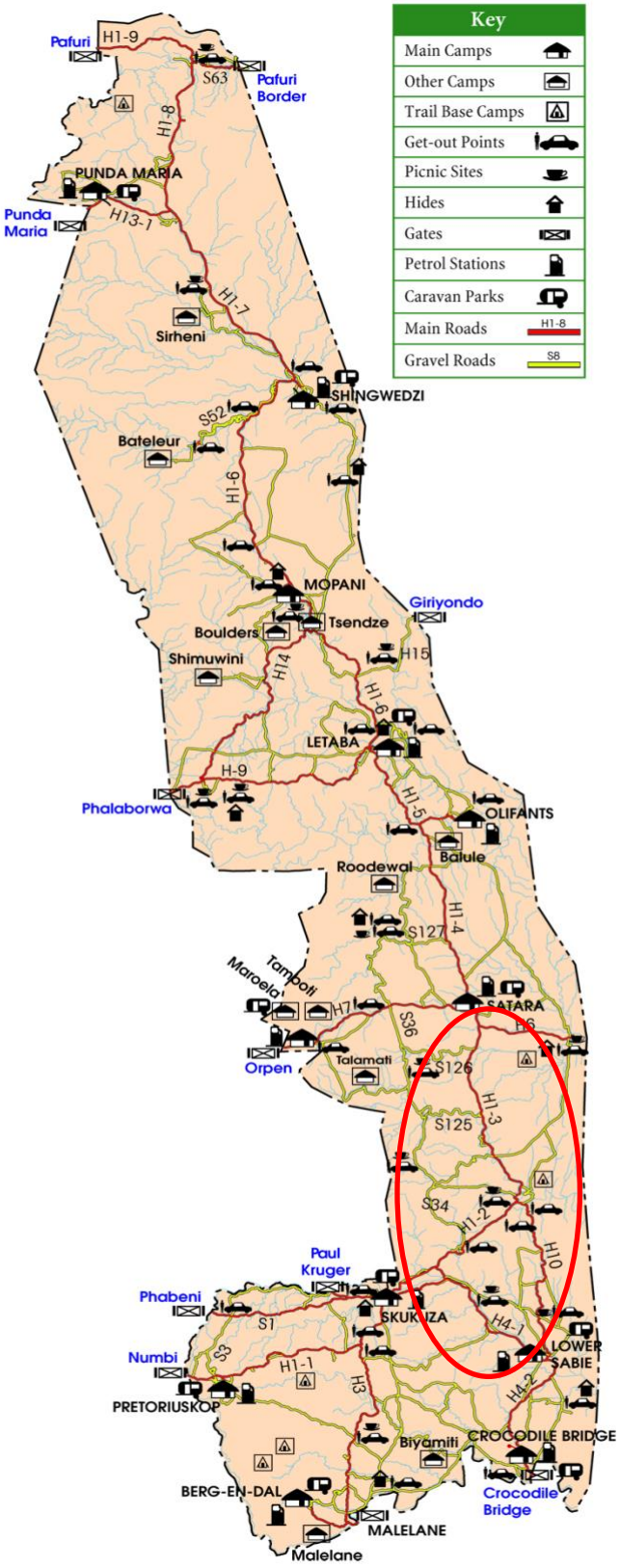


Figure 1.1: Kruger National Park Map showing main camps. Study area circled. Map sourced from https://www.sanparks.org/parks/kruger/tourism/map.php.

Figure 1.2: Photo of pre-drought vegetation in the Tshokwane region of Kruger National Park, 2001, wet season

Figure 1.3: Photo of pre-drought vegetation in the Tshokwane region of Kruger National Park, 2001, dry season

Figure 1.4: Post-drought conditions in the Tshokwane region of Kruger National Park, August 2018

## *Chapter descriptions*

My thesis consists of this general introduction, three manuscript chapters and a general discussion and conclusion.

Chapter 2 tests if giraffe females change their foraging behaviour in relation to their immediate social group and their nearest neighbours and if this is influenced by season. I determine if females change their foraging efficiency if a large male is present, therefore determining if there a foraging cost to being near large males.

Chapter 3 tests if foraging behaviour is changed with food availability caused by drought. Original data collected by Cameron & du Toit (2005) was obtained while food was plentiful, while the new data was collected after seven years of drought. After periods of drought there is less food available which may now mean that females could be less choosy with whom they forage near as there are fewer foraging options. They may now have a higher tolerance for large males close to them. Environmental variability on giraffe foraging will be discussed.

Chapter 4 tests measures the sexual segregation in giraffe populations and tests whether the degree of segregation changes with environmental and food availably differences. I also test a range of hypotheses to determine what influences horizontal segregation in the KNP giraffe population. I hypothesise that giraffe will segregate less horizontally when there is less food available. The social segregation index is used to determine if the giraffe in the area change their segregation after the drought.

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# Chapter 2: Effects of close neighbours and group size on foraging behaviour in giraffe (*Giraffa camelopardalis)*

## *Introduction*

Animals form groups for a variety of reasons including reducing predation risk (Powell, 1974; Pulliam, 1973; Silk, 2007), finding food (Clark & Mangel, 1986; Silk, 2007) and increasing mating opportunities (Silk, 2007; Westneat et al., 2000). However, there are also costs to living in a group, such as increased competition (Krause & Ruxton 2002; Silk, 2007), greater disease transmission (Hoogland, 1979; Van Vuren, 1996) and becoming more conspicuous to predators (Cresswell, 1994; Krause & Ruxton, 2002). Social behaviours can both increase and decrease the costs of group living through phenomena such as dominance hierarchies (Sachser et al., 1998). Social behaviours can have effects on many aspects of an animal's ecology and persistence, including mating systems and associated mating behaviours which can then influence the genetic structure of a population and therefore its viability (Blumstein, 2010). However, the role of these social behaviours within groups in ecology is often overlooked.

Group living and the associated presence of close neighbours can have substantial costs for individuals. There is an increase in competition for resources, as more individuals will be competing for the same food supply in the area (Krause & Ruxton, 2002). The more individuals trying to share the resource, the smaller the per capita share is (Krause & Ruxton, 2002). There is also increased competition for potential mates, as there will now be more rival individuals competing for a limited number of mates (Silk, 2007). When living in a group with other individuals there is a higher risk of becoming infected with a disease or parasite (Silk, 2007), which will increase infection rate (Hoogland, 1979). Grouping increases conspicuousness to predators, as larger groups are easier to locate than single animals (Silk, 2007). Some predators, such as sparrowhawks (*Accipiter nisis*), are known to preferentially target larger groups (Cresswell, 1994). When other individuals are present, there is an increased need for social vigilance, with the within group surveillance hypothesis suggesting that vigilance functions are used to protect individuals from conspecific competitors as well as predators (Alberts, 1994; Renouf & Lawson, 1986; Yáber & Herrera, 1994). Negative social interactions such as harassment could also increase in frequency (Clutton-Brock & Parker, 1995), and aggression in general may also increase (Krause & Ruxton, 2002). For example, in groups with hierarchy systems, there will be more individuals that could

challenge the dominant animal and more fights could occur (Krause & Ruxton, 2002). Despite these costs, groups are still frequent, suggesting the benefits often outweigh the costs.

The benefits of groups and neighbours on individuals include providing greater protection from predators with higher collective vigilance rates (Powell, 1974; Pays et al., 2009), predator swamping (Sweeney & Vannote, 1982) and communal defence (Bertram, 1975). Groups improve success in locating or maintaining access to patchy resources (Creel & Creel, 1995), and create mating opportunities (Silk, 2007; Westneat et al., 2000). Social interactions with neighbours can provide fitness and health benefits. In macaque monkeys (*Macaca mulatta*), immune competence was improved in individuals that spent more time in association with other animals (Kaplan et al., 1991). A reduction in female stress occurs in baboon populations where females form close relationships with other individuals (Wittig et al., 2008). Social relationships can also increase the reproductive success of animals, as seen in horses (Cameron et al., 2009), dolphins (Frère et al., 2010) and baboons (Silk et al., 2003). Thus, there are a range of positive and negative outcomes from group membership as well as associates within a group. Furthermore, the social relationships between neighbours may mitigate the costs of grouping. For example, close social bonds can reduce harassment associated with group living (Cameron et al., 2009).

Since social relationships can both mitigate and increase impacts, the closest neighbour may be more important than the group composition itself when it comes to social effects on individuals (Rolando et al., 2001). This would give us the ability to use nearest neighbor or proximity measures to describe social preferences (Bashaw et al., 2007). Furthermore, individuals may be experiencing both group effects and neighbour effects, and so they both need to be measured to understand social groups. Most work on positive and negative effects of neighbours and social bonds focus on long-term stable groups, with fission-fusion systems largely overlooked (Silk, 2007). Fission-fusion systems may better demonstrate the proximal cues for grouping as individuals change group composition repeatedly, potentially responding to immediate costs and benefits. Studies have also focused on groups and social networks, not direct costs and benefits of your current social group.

Harassment behaviour by a close neighbour can affect an individual. It is a form of sexual coercion by males that involves repeated attempts to copulate or monopolize females in the hope of trying to induce them to mate immediately, with costs to females in time, energy or even injury (Clutton-Brock & Parker, 1995). This harassment behaviour can affect many aspects of a female's behaviour including her level of vigilance. Individual vigilance behaviour can be altered by social partners, which involves both a time and energy cost, as time spent vigilant is usually at the expense of foraging (Cameron & du Toit, 2005). Although more usually associated with anti-predator behaviour, vigilance is also used to monitor and detect intraspecific risks (Artiss & Martin, 1995; Slotow & Coumi, 2000). This increased vigilance towards conspecifics implies there could be costs to having a close neighbour present, due not only to harassment, but foraging costs associated with monitoring these individuals. Feeding and foraging behaviour can also be affected by harassment, by reducing the amount of time a female can feed in the presence of a male, often due to vigilance (Agrillo et al., 2006; Schlupp et al., 2001). However, if neighbours are known or preferred individuals (or potentially kin), levels of harassment experienced may decrease (Tibbetts & Dale, 2007; Rankin, 2011).

Giraffe are an ideal species to look at harassment and social effects in a fission-fusion species as male harassment is frequent due to their breeding strategy, but individuals can chose to leave the group. Giraffe are non-seasonal breeders, so females can come into oestrous at any time during the year (Bercovitch et al., 2006) making them asynchronous. Consequently females do not come into oestrous at the same time (Dagg & Foster, 1976). They have a polygynous mating system so males have to adopt a roaming reproductive strategy to be able to find and then guard their potential mates (Bercovitch et al., 2006). It is thought that only 6-11% of female giraffe are receptive for breeding at any given time (Brand, 2007), making it difficult for males to find mates. Therefore males look for a receptive female in oestrus by urine testing, which involves a bull soliciting a urine sample from the cow by sniffing and nuzzling her genitalia (du Toit, 2001). Seeber et al. (2013) suggest that giraffe bulls undergo unsynchronized rut-like periods like other species where males tend to roam to find mates, such as elephants. These periods may be similar to an elephant's period of musth but last for only days instead of months seen in elephants (Seeber et al., 2013). When elephant bulls are in musth the females become increasingly

wary and males will chase females when they are in oestrous (Moss, 1983). This clearly shows that male elephants harass females when in musth (Chelliah & Sukumar, 2015). This harassment can then be disruptive to females in many of their daily behaviours. Female giraffe will increase vigilance behaviour when large males are present in their group, and this could incur a foraging cost (Cameron & du Toit, 2005). However, the effects of males in close proximity has not yet been investigated.

This chapter aims to determine the effect of a close neighbour on foraging behaviour of female giraffe, and I test if there is seasonal variation in these effects. I aim to test if females change the amount of time they spend at a patch of food or their foraging investment if a large male is present, therefore determining if there a foraging cost to being near large males. I hypothesise that female giraffe will avoid feeding near mature bulls to avoid harassment, increased vigilance and foraging loss.

## *Methods*

Data was collected in the Tshokwane region of Kruger National Park, South Africa, based around the ranger station (24° 47'S, 31° 52'E), between July 2001 and July 2002 by Cameron & du Toit (2005). 455 groups were encountered, with a total of 1639 giraffe. The region had undergone a large flood year in 2000 so there was high food availability for the collection period. The vegetation in the area was dominated by *Acacia nigrescens* and *Sclerocarya birrea* trees (Cameron & du Toit, 2005). In the Southern African region, there are two distinct seasons; a wet and a dry season. The winter is dry with little to no rainfall. The summer months have abundant rainfall. This variation in in rain and temperature then influences the food availability in the area. Food is usually plentiful in the wet months with vegetation drying up and dying in the dry season.

Giraffe were located opportunistically while driving along public roads during daylight hours. Group composition and size was recorded, with all individuals within 100m of each other considered to be members of the group (van der Jeugd & Prins, 2000) consistent with other studies. A focal female was chosen based on whether they were foraging, and then the

foraging behaviour of that individual was recorded. Females were chosen as focal individuals as they are affected by the harassment from males and will give a good indication if this behaviour affects foraging efficiency. Neck angle of the giraffe and number of bites taken while foraging were both recorded. Length of each foraging 'episode' was recorded. An episode was defined as all continuous bites at one neck angle (Cameron & du Toit, 2005). An episode was terminated when the individual giraffe changed its neck angle or by ending foraging to perform another task such as scanning, moving or grooming (Cameron & du Toit, 2005). With episode length and number of bites per episode recorded it was possible to calculate a bite rate in bites per second, both excluding and including scanning time. This also enabled me to calculate the percentage forage efficiency lost to scanning.

The identity of the nearest neighbours (within 10m of focal individual) were recorded, along with the estimated distance between the individuals. However, using nearest neighbor as a measure can have some problems. Firstly, since the distance to the nearest neighbor can differ, each neighbour cannot be assumed to have a similar effect (Cameron & du Toit, 2005). Furthermore, several individuals may be close to the focal animal, so it cannot be assumed that the nearest neighbor is the only individual affecting behaviour (Cameron & du Toit, 2005). We recorded all individuals and their distances as you can measure the influence of individuals that are within interacting distance. We then defined near neighbours as any individual within 10m of the focal individual.

*Data analysis*

Bites/sec and bites/sec including scanning were calculated from the data to establish bite rate. Bite rate is used as a measure of foraging efficiency (Cameron & du Toit, 2005; Cash & Fulbright, 2005; Ruckstuhl et al., 2003). Bites/sec was calculated by dividing number of bites by the episode length (referred to from here as foraging efficiency). Bites/sec including scans was calculated by diving the number of bites by the episode length plus the time spend standing and looking/scanning after the foraging episode. This gives us a measure that takes into consideration how stopping and scanning affects the foraging efficiency of an

individual (referred to from here as foraging efficiency including scans). I also calculated the time cost of vigilance, as the proportion of time added to an episode by scanning.

All data was checked to ensure that it confirmed to a normal distribution. Linear interaction models were performed in R Studio, with the lme4 and lmerTest packages (Douglas et al., 2015; Kuznetsova et al., 2017), and used to investigate if there was an effect of having a close neighbour present on the foraging efficiency of a female giraffe and if the identity of that close neighbour had an effect. The response variables were average bites per second (foraging efficiency), average bites per second including scans (foraging efficiency including scans) or proportion time cost, with close neighbour (present or absent), neighbour ID (male, female or calf close neighbour) and season (wet or dry) as fixed factors. This was performed for all data with female giraffe as focal individuals.

## *Results*

### Overall data period

*Group size with calves*

Group size for female giraffe with and without calves was determined. Female giraffe were found predominately in smaller groups when they had a calf present (Table 2.1).

Table 2.1: Pre-drought average group sizes for female giraffe with and without a calf present

| | **With Calf** | **Without calf** |
|---|---|---|
| Female group size | 2.44 | 3.12 |

*Foraging efficiency*

The mean bite per second was 0.327 seconds. Females with a close neighbour (within 10m) forage less efficiently than an individual with no close neighbour. There was a significant

interaction between the presence of a close neighbour and season (Table 2.2). Females with male neighbours forage less efficiently than with female or calf neighbours.

Table 2.2: Mixed linear model results for foraging efficiency for the overall pre-drought period, df = 3613

| | **t value** | **p value** |
|---|---|---|
| Close Neighbour (any) | 5.35 | <0.001 |
| Season | 0.23 | 0.81 |
| Close Neighbour:Season | 3.71 | <0.001 |
| Female Neighbour | 5.13 | <0.001 |
| Male Neighbour | 2.27 | 0.02 |
| Calf Neighbour | 0.16 | 0.86 |
| Female Neighbour:Season | 3.91 | <0.001 |
| Male Neighbour:Season | 1.05 | 0.29 |

*Foraging Efficiency including scans*

The mean bite per second per episode including any vigilance was 0.28 seconds. Female giraffe were significantly less efficient with a close neighbour. The effect of season was also significant. There was a significant interaction between the presence of a close neighbour and season (Table 2.3).

Table 2.3: Mixed linear model results for foraging efficiency including scans for the overall pre-drought period, df = 3601

| | **t value** | **p value** |
|---|---|---|
| Close Neighbour (any) | 3.44 | <0.001 |
| Season | 2.04 | 0.04 |
| Close Neighbour:Season | 3.97 | <0.001 |
| Female Neighbour | 3.31 | <0.001 |
| Male Neighbour | 1.35 | 0.17 |
| Calf Neighbour | 0.43 | 0.66 |
| Female Neighbour:Season | 4.88 | <0.001 |
| Male Neighbour:Season | 0.96 | 0.33 |

*Proportion time cost of vigilance*

Vigilance increased foraging time by 12%. There was a significant difference in proportion time cost for females with male neighbours, with female giraffe with male neighbours having an 8% increase to foraging time (Table 2.4).

Table 2.4: Liner model results for proportion time cost for the overall pre-drought period, df = 5540

| | **t value** | **p value** |
|---|---|---|
| Close Neighbour (any) | 1.57 | 0.11 |
| Female Neighbour | 3.40 | <0.001 |
| Male Neighbour | 4.94 | <0.001 |
| Calf Neighbour | 1.19 | 0.23 |

## Seasonal Variation

There were significant effects of season and significant interactions with season and both variables, therefore the main effects in the different seasons were analysed separately.

Wet season

*Foraging efficiency*

The mean bite per second in the wet season was 0.327 seconds. There were no significant effects for any variable for foraging efficiency in the wet season (Table 2.5). However, female giraffe with close neighbours are more efficient than those without a neighbour, particularly with a female neighbour. While not significant, females with male neighbours were less efficient than with female or calf neighbours.

Table 2.5: Linear model results for foraging efficiency in the wet season, df = 1080

| | t value | p value |
|---|---|---|
| Close Neighbour (any) | 1.10 | 0.27 |
| Female Neighbour | 1.61 | 0.10 |
| Male Neighbour | 0.81 | 0.41 |
| Calf Neighbour | 0.22 | 0.82 |

*Foraging efficiency including scans*

The mean bite per second in the wet season was 0.266 seconds when vigilance scans were incorporated. Female giraffe were significantly more efficient with a close neighbour (Table 2.6). Females with male neighbours were significantly less efficient than with female or calf neighbours.

Table 2.6: Linear model results for foraging efficiency including scans for the wet season, df = 1071

| | t value | p value |
|---|---|---|
| Close Neighbour (any) | 2.76 | 0.005 |
| Female Neighbour | 4.04 | <0.001 |
| Male Neighbour | 2.88 | 0.003 |
| Calf Neighbour | 0.48 | 0.62 |

*Proportion time cost of vigilance*

Vigilance increased foraging time by 17%. There were significant effects for both male and female neighbours (Table 2.7). Female giraffe with male neighbours have an 11% foraging cost.

Table 2.7: Liner model results for proportion time cost in the wet season, df = 1000

| | t value | p value |
|---|---|---|
| Close Neighbour (any) | 2.20 | 0.028 |
| Female Neighbour | 3.55 | <0.001 |
| Male Neighbour | 3.74 | <0.001 |
| Calf Neighbour | 0.78 | 0.434 |

Dry season

*Foraging efficiency*

The mean bite per second in the dry season was 0.326 seconds. Female giraffe are less efficient when a close neighbour is present (Table 2.8). Females with male neighbours are also significantly less efficient than with female neighbour (Figure 2.1).

Table 2.8: Linear model results for foraging efficiency in the dry season, df = 2530

| | **t value** | **p value** |
|---|---|---|
| Close Neighbour (any) | 5.05 | <0.001 |
| Female Neighbour | 4.84 | <0.001 |
| Male Neighbour | 2.16 | 0.03 |

*Foraging efficiency including scans*

The mean bite per second in the dry season was 0.28 seconds when vigilance scans were incorporated. The effect of a male neighbour was not significant (Table 2.9), with females with male neighbours were less efficient than with female neighbour (Figure 2.2).

Table 2.9: Linear model results for foraging efficiency including scans in the dry season, df = 2522

| | **t value** | **p value** |
|---|---|---|
| Close Neighbour (any) | 3.28 | 0.001 |
| Female Neighbour | 3.17 | 0.001 |
| Male Neighbour | 1.29 | 0.19 |

*Proportion time cost of vigilance*

Vigilance increased foraging time by 12%. There were no significant differences in the proportion time cost for any of the factors (Table 2.10).

Table 2.10: Liner model results for proportion time cost in the dry season, df = 2517

| | t value | p value |
|---|---|---|
| Close Neighbour (any) | 1.45 | 0.14 |
| Female Neighbour | 1.40 | 0.16 |
| Male Neighbour | 0.60 | 0.54 |

*Seasonal Comparisons*

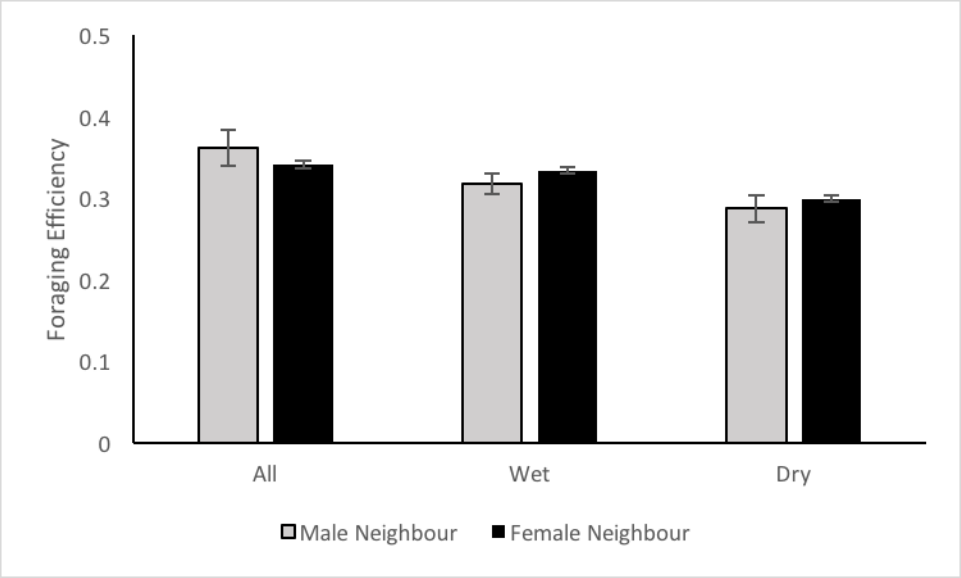


Figure 2.1: Foraging efficiency for female giraffe with a male vs a female neighbour for all data periods, showing seasonal variation

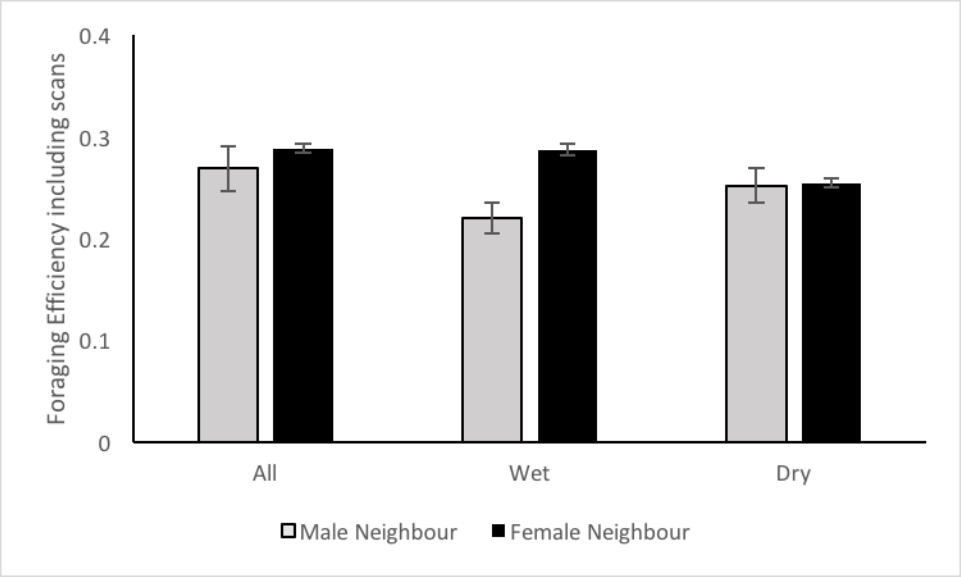


Figure 2.2: Foraging efficiency including scans for female giraffe with a male vs female neighbour for all data periods, showing seasonal variation

## *Discussion*

### *Overall Effects*

Within a group, a female giraffe's foraging is more efficient when she has no close neighbours, with longer foraging episode lengths and a higher foraging efficiency when there was no close adult neighbour within 10m of her, regardless of neighbour identity. Therefore, both sexes could present a similar risk in loss of foraging due to competition or harassment. Having a close male neighbour would increase the risk of male harassment if he was to check if she is in oestrous. A female giraffe that is in oestrous may pose an equal risk to foraging efficiency as this female may attract male bulls. A male who is attracted to the female in oestrous will more than likely check all females in the vicinity to optimise his mating opportunities (du Toit, 2001). A non-oestrous cow may therefore benefit from moving away from females in oestrus (Cameron & Du Toit 2005). Individuals may also be monitoring neighbours for competition of foraging patches (Beauchamp, 2015).

Female giraffe are more vigilant when there are adult males in their group (Cameron & Du Toit 2005). Females check where the male is and how close he is and we have now verified that this does cause them to forage less efficiently. If a male is the close neighbour she will then have to keep looking at him to be able to move away in time if he starts to harass her therefore having a higher foraging cost. Recently Muller et al. (2018a) found that female giraffe only show a social preference when foraging. They also suggest that adult females may associate with other females that also want to forage instead of foraging near males, as it is too costly (Muller et al., 2018a).

When a female giraffe has a calf as a close neighbour (more than likely to be her own) there is no significant effect in foraging efficiencies. However, there is a slight increase in foraging efficiency including scans. The calf poses no risk of harassment and this reduces the need to scan for conspecifics. Female giraffe have been found to be in smaller groups when they had calves present (Muller et al, 2018b). In smaller groups, they will need to spend less time watching conspecifics and therefore will be more efficient at foraging. I also found the same effect, females with calves were in smaller groups on average than females without calves. This is contrary to the theory that female giraffe may form 'crèches' with their young (Langman, 1977).

Giraffe have a very high calf mortality rate, with only about half of all calves born survive their first year (Bercovitch & Berry, 2010; Dagg & Foster, 1976). This rate is observed in Kruger National Park, with 48% of all calves dying (Fourie, 2014). This high rate of mortality probably arises from lion predation (Dagg & Foster, 1976). If a female is foraging more and is less vigilant when she has a calf present than this may help explain the high mortality rate. Females with calves are more nutritionally restricted, needing a larger quantity of food than normal to be able to sustain milk production for a calf (Deacon et al., 2015). If a female needs to consume more food she therefore becomes restricted in the amount of time so can devote to vigilance behaviour.

*Seasonal variation*

When data was broken down to look at the wet and dry season individually, we saw that giraffe have longer episode lengths in the wet season. This means they are staying at a particular spot and tree for longer periods. There is more food available so there is no need to waste energy to go to another tree when there is plenty of food available. This may also relate to there being fewer tannins in foliage during the wet season, as the onset of rain means that plants start rapidly growing young leaves which contain lower levels of tannins (Herms & Mattson, 1992; Styles & Skinner, 1997). With less chemical defences from the tree they don't have to go to find a more palatable tree, as giraffe avoid trees with high tannin levels (Caister et al., 2003; Furstenburg & Van Hoven, 1994).

In the wet season, there were significance differences in foraging efficiencies including scans only. The ample food might result in no environmental limitations on their efficiency. However, when scans are incorporated, female giraffe were less efficient when they had a male close neighbour. This is reinforced with a higher percentage cost of vigilance in the wet season with male neighbours. Therefore, when food is plentiful, females are less tolerant of male giraffe close to them and we see much more of a harassment effect. Plentiful food means that reproductive efforts can proceed with enough resources to sustain a healthy pregnancy (Deacon et al., 2015). In certain populations more fertile females can be encountered during the wet season (Wolf et al., 2018). Therefore, if a male is more likely to encounter a receptive female in the wet season then the risk of harassment in this period would be higher. This would fit with our data showing that female giraffe become less efficient when males are around.

When female giraffe have another female giraffe next to them they became significantly more efficient at foraging in the wet season. Other cows do not pose an immediate harassment effect and females may prefer to associate with other females while foraging as this has lower foraging costs than male neighbours (Muller et al., 2018a). It could also be that if another individual is close that this may increase the perceived competition for that individual and they forage more efficiently to outcompete their neighbour (Mitchell et al.,

1990; Roberts, 1996). Female giraffe were also more efficient with a close neighbour present, which may be caused by the same reasons.

During the dry season there was no significant difference in a male vs female neighbour for female giraffe in foraging efficiency including scans. This shows that in the dry season with less food available that female giraffe become more tolerant of close male neighbours, and harassment has less of an effect on female foraging. Females may already be pregnant in the dry season as copulation may have occurred in the wet season (Wolf et al., 2018). This then means the male may no longer be interested in those females (Wallen et al., 2015) and no longer pose a threat of harassment. There was a slight significant effect with female giraffe less efficient with a male neighbour when foraging efficiency was considered but this may simply be an artefact of the fact the males are larger and could just generally be more efficient than a female giraffe (Ginnett & Demment, 1997; Kotze, 2007).

These seasonal results support the findings of Cameron & du Toit (2005), that vigilance of conspecifics does influence the foraging efficiency of giraffe and is an important factor to consider when looking at giraffe social interactions. Both the wet and dry season significance results are seen in the foraging efficiency including scans which signifies the increased presence of vigilance behaviour. In the wet season, we see a significant difference in female giraffe with male vs female neighbours. Female giraffe were less efficient when their close neighbour was a male as she will keep looking at him to avoid that harassment behaviour. A female has more of an opportunity to leave the area and find more food in the wet season as food is plentiful but in the dry season she no longer has this option. In the dry season, there was no significant difference in the foraging efficiency of a female giraffe with male vs female neighbours as the need to acquire food could outweigh the cost of males.

## *Conclusion*

We have shown that there is an effect of close neighbours on the foraging efficiency of giraffe females. A female will forage less efficiently when she has a close neighbour and become more vigilant and less efficient when that close neighbour is a male. Close neighbours have a large effect on individual behaviour and should be incorporated into studies looking at social aspects of giraffe groups.

There is an increase in tolerance for male close neighbours with a reduction in food availability due to season. This effect could become more pronounced with the development of drought conditions. Drought is a common occurrence in the Southern Africa region and can completely alter the composition and availability of the flora that is available for foraging (Vetter, 2009). If there is less food available, a female may become less aware and vigilant towards close neighbours, and allow individuals and males to forage closer to her. This will be explored in Chapter 2.

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# Chapter 3: Effects of food limitation on social behaviours and foraging efficiency in giraffe (*Giraffa camelopardalis)*

## *Introduction*

Groups provide benefits to individuals but can also have fitness costs, and so groups are seen when costs outweigh benefits, reviewed in (Silk, 2007). One type of social structure is fission-fusion, where individuals come and go from the group with no apparent permanent bonds (Dagg, 2014). Diverse species exhibit this structure, including ungulates like the giraffe (Dagg, 2014), marine mammals like bottlenose dolphins (Smith et al., 2016), in primates including chimpanzees (Lehmann & Boesch, 2004) and marsupials such as the eastern grey kangaroo (Carter et al., 2009). The fluidity of fission–fusion social systems allows individuals to counterbalance negative consequences of grouping by splitting in small groups but then aggregate again when it is beneficial (Popa-Lisseanu et al., 2008). Fission-fusion grouping allows for flexibility in group size and composition so that changes can be made in response to changing environmental conditions (Popa-Lisseanu et al., 2008). For example, groups may dissolve in response to resource limitation, decreasing competition for unpredictable and patchy food resources (Couzin & Laidre, 2009). These groupings offer an opportunity to be able to gain insights into the costs and benefits of grouping, as members can respond immediately to any situations that could be costly, usually resulting in a fission event. They can also determine when conditions become beneficial for grouping to occur, by an increase in fusion events.

Previous studies have looked at social grouping and networks but tend not to look at how the identity of a close neighbour can affect the individual or the direct costs and benefits of your current social group. The distance to and identity of an individual's closest neighbour may be more important than the group size or composition itself when it comes to social effects on individuals (Rolando et al., 2001), particularly in a fission-fusion group. As it is hard to determine the membership of a group within a fission-fusion species, close neighbour identity gives a clearer indication of social interactions. Feeding and foraging behaviour can be affected by social interactions. For example, harassment can cause a female to reduce the amount of time she can feed in the presence of a male (Agrillo et al., 2006; Schlupp et al., 2001). Foraging is a key activity an animal needs to perform to survive (Pellew, 1984), and it is important to understand the influence of multiple feeders on foraging success.

Seasonal variation in forage presents important challenges but incidents of drought can dramatically limit the amount and composition of vegetation beyond seasonal effects (Thurow & Taylor, 1999). Plant mortality occurs due to water stress and subsequent carbon starvation (McDowell, 2011). With the amount of vegetation decreasing, food availability for the herbivorous animals also declines (Thurow & Taylor, 1999; Favreau et al., 2018). Food is a key factor in regulating populations of ungulates in African savannas (Shorrocks, 2016), as indicated by the correlation between rainfall and ungulate biomass (Coe et al., 1976). Africa has a long history of rainfall fluctuations of varying lengths and intensities (Gommes & Petrassi, 1996). However, the occurrence of drought and other extreme weather events are predicted to increase with the progression of climate change effects (Watson & Albritton, 2001). Therefore, a better understanding about how these events affect the animals in the areas will help in creating management plans to cope with the impacts on the ecosystem.

A limited supply of food will increase both inter- and intra- specific competition. Individuals will compete more for remaining small amount of food (Cappuccino & Price, 1995). In the dry season, competition is the most intense (Simmons & Scheepers, 1996), and after drought conditions where the limitation of food will be more severe than an ordinary dry season, competition will further increase (Cappuccino & Price, 1995). This may cause individuals in a fission-fusion system to alter their current groupings to adjust to the limited food supply. By leaving the group individuals will decrease competition at that patch of food, and if they can find another suitable patch, will be able to consume more (Couzin & Laidre, 2009). However, if there are no other suitable food sources nearby it may increase the need to group to gain access to the remaining food.

When food becomes limited, the amount of energy an individual is able to obtain while foraging is also decreased (French et al., 2007). When energy limitation occurs, non-essential processes are inhibited (French et al., 2007), with resources most often being diverted from non-essential systems to systems required for immediate survival (Vera et al., 2017). Reproduction can be suppressed, sometimes because the physical condition of the female limits the ability to become pregnant or support a foetus (Mitchell et al., 2010). If

reproductive behaviours are suppressed, the corresponding male breeding behaviours may likewise be reduced, potentially decreasing the amount of harassment towards females.

Giraffe are very large ruminants that have to spend a large amount of time feeding to meet daily intake requirements (du Toit & Yetman, 2005). The required amount of forage for a mature giraffe is 50kg of browse daily (to provide 150 000 kj energy) (Mitchell et al., 2010). Giraffe are considered to be 'exclusive browsers', feeding on plants and shrubs 2-5m above the ground (Seeber et al., 2012), but they can very occasionally graze on grass. When doing this they must use the same splayed leg posture they adopt for drinking (Seeber et al., 2012). This position means they are particularly vulnerable to attack from predators (Périquet et al., 2010). With a lack of browsing opportunity following drought conditions this may increase the frequency of grazing but seeing as it is a risky position this may not occur.

Giraffe occur in fission-fusion groups that allow for flexibility in grouping that can adjust to changes in food availability (Carter et al., 2013; Dagg, 2014). Drought conditions could change the influence that social factors have on foraging behaviours as the environment and resource abundant changes dramatically. Seasonal variations in giraffe group composition and herd size occur (Brand, 2007; Fennessy, 2004; Wolf et al, 2018), and I showed that there is a seasonal effect on the social interactions between individuals (Chapter 2). Drought events could then intensify these seasonal effects on social interactions. Giraffe may be less vigilant towards conspecifics during or post-drought then they are during normal seasonal variation as the lower food availability will limit foraging options, forcing individuals to stay with other giraffe if browsing options are limited. Male harassment is a common behaviour observed in giraffe fission-fusion populations due to their polygynous system the means males have to adopt a roaming reproductive strategy to be able to find and then guard their potential mates (Bercovitch et al., 2006). Males must continuously be looking for receptive females by urine testing behaviours which can be invasive to the female (du Toit, 2001). Harassment may change with food availability and a drop could result in less male harassment towards females or females could become less concerned with these advances. Loss of foraging options may now mean that female giraffe could be less choosy with whom they forage near and they may now have a higher tolerance for large males close to them.

The aim of this chapter is to determine if there is an effect of drought-induced food shortages on the social interactions between close neighbour that were found in Chapter 2. I also aim to determine if grouping patterns and response to group members change with this food restriction. I hypothesise that after a period of drought (2015/2016) and while the vegetation recovers, females will become less choosy and allow bigger males to forage closer to them than pre-drought due to reductions in foraging options, which is predicted to reduce foraging efficiency.

## *Methods*

Data has been collected over two separate periods but in the same area. The first was collected between July 2001 and July 2002 by Cameron & du Toit (2005). This collection was made the two years following a large flood event in 2000. 455 groups were encountered, with a total of 1639 giraffe. With large amounts of water present the previous year, the growth for the following seasons was high. Vegetation was plentiful and looked to be of a high quality. Since this period, Kruger National Park has undergone a sustained period of drought over a two-year period from 2014 until 2016. The wet season of 2014/2015 saw only 255mm fall which is only 65% of the yearly average (South African National Parks – SANParks – Official Website, 2019). It became even worse the following year with the 2015/2016 season only having 190mm rain as opposed to the normal 550mm (52% of the normal average) (South African National Parks – SANParks – Official Website, 2019). The 2016/2017 season saw an increase in rainfall with 371mm falling (South African National Parks – SANParks – Official Website, 2019), which is still less than average. The 2018 dry season has been particularly hot and dry again with the onset of the rainy season not starting until November, a month later than normal. This drought has dramatically changed the vegetation cover and food availability in the park. The habitat was previously dominated by woody vegetation but post drought has become a more open grassland (E. Cameron, personal communication, September 2017; Figure 1.4), aided in part by elephants knocking down trees at greater rates in times of drought (Bax & Sheldrick, 1963). Vegetation in the

area consists of mixed woodlands, comprised mainly of acacia and marula species, and open savannah grasslands.

The second data set was collected in Kruger National Park in August and September 2018. Observations were carried out over 22 days with 162 giraffe groups encountered, and a total of 758 individual giraffe. A research permit was obtained from Kruger National Park Scientific Services, reference SUTN1535. During both periods, giraffe were located opportunistically while driving public roads between Satara, Skukuza and Lower Sabie Rest Camps during daylight hours. Routes were varied each day so the same roads were not driven at the same time each day. Observations were made from inside a vehicle due to safety regulations of Kruger National Park. Giraffe are habituated to the presence of vehicles due to the large number of tourist vehicles they encounter, therefore the effect of our presence while observing would be minimal.

Once giraffe were located, group composition and size was recorded, with all individuals within 100m of each other considered to be members of the group (van der Jeugd & Prins, 2000), consistent with other studies. However, this classification is arbitrary as what we perceive as a group may not be relevant to a giraffe (as discussed in Chapter 2). A focal female was chosen based age and their visibility for data collection, as well as whether they were currently foraging. Only adults were chosen for observations as they would be sexually mature and subject to oestrous and mating behaviours and would be members of the core group. Females were chosen as focal individuals as they are affected by the harassment by male and will give a good indication if this behaviour affects foraging efficiency. The identity of the nearest neighbour (within 10m of focal individual) was recorded, along with the estimated distance between the individuals.

The number of bites were then recorded with the duration of a foraging episode. An episode was defined as all bites taken at the same head height and position on the tree. An episode was deemed finished when the individual moved their head to a new position on the tree, moved to a new tree or performed another act such as scanning or grooming. Time spent standing, chewing or scanning after an episode was also recorded. Data was collected from individuals until they moved out of view for an extended period (>15/20 minutes).

Most observation periods ranged from 10 to 60 minutes, with an average of 30 minutes per observation.

*Data analysis*

Bites/sec and bites/sec including scanning were calculated from the data to establish bite rate. Bite rate is used as a measure of foraging efficiency (Cameron & du Toit, 2005; Cash & Fulbright, 2005; Ruckstuhl et al., 2003). Bites/sec was calculated by dividing number of bites by the episode length (referred to from here as foraging efficiency). Bites/sec including scans was calculated by dividing the number of bites by the episode length plus the time spend standing and looking/scanning after the foraging episode. This gives us a measure that takes into consideration how stopping and scanning affects the foraging efficiency of an individual (referred to from here as foraging efficiency including scans). I also calculated the time cost of vigilance, as the proportion of time added to an episode by scanning.

All data was checked to ensure that it confirmed to a normal distribution. ANOVAs were conducted in R Studio to determine significant differences in group sizes and TukeyHSD tests run to determine where the significance occurred. Linear interaction models were performed in R Studio, with the lme4 and lmerTest packages (Douglas et al., 2015; Kuznetsova et al., 2017), and used to investigate if there was an effect of having a close neighbour present on the foraging efficiency of a female giraffe and if the identity of that close neighbour had an effect. The response variables were average bites per second (foraging efficiency), average bites per second including scans (foraging efficiency including scans), proportion time cost or episode length, with close neighbour (present or absent) and neighbour ID (male, female or calf close neighbour) as fixed factors. This was performed for all data with female giraffe as focal individuals.

## *Results*

### *Group Size and Composition*

Average group size was calculated for each data set; pre-drought overall 2001/2002, the pre-drought wet season, the pre-drought dry season and post-drought. There is little difference in group sizes, with a slight decrease in group sizes post-drought (Table 3.1), but the differences were not significant (ANOVA, F=0.437, p >0.05).

Table 3.1: Group Size comparisons of all data periods

| | **All Groups (including lone individuals)** | **Groups with >1 giraffe** | **% Alone** |
|---|---|---|---|
| Pre-drought Overall | 3.64 | 4.93 | 33% |
| Pre-drought Wet | 3.81 | 4.93 | 30% |
| Pre-drought Dry | 3.55 | 4.91 | 35% |
| Post-drought | 3.48 | 4.75 | 30% |

The composition of giraffe groups shows little change between seasons pre-drought. There was a decrease in the size of mixed sex groups and an increase in the size of male only groups post-drought (Table 3.2). An analysis of variance (ANOVA) showed significant variation between groups (F = 16.39, P = <0.001). A post hoc Tukey test showed a significant difference in male group size between pre-and post-drought data (p= <0.001).

Table 3.2: Average group sizes for different group compositions for all data periods

| | **Mixed Sex Groups** | **Female Only Groups** | **Male Only Groups** |
|---|---|---|---|
| Pre-drought Overall | 6.14 | 3.23 | 1.3 |
| Pre-drought Wet | 6.13 | 3.49 | 1.29 |
| Pre-drought Dry | 6.14 | 3.07 | 1.3 |
| Post-drought | 5.6 | 2.5 | 2.3 |

### *Episode Length*

The mean episode length for post-drought data, was 49.9 seconds, which did not vary with neighbour identity (Table 3.3). However, an increase in episode length was noted for all

types of neighbour compared to pre-drought data (Figure 3.1). There is a significant difference in length of duration between the pre-drought and post-drought periods, Wilcoxon rank sum test (W=3302400, p = <0.001), with post-drought episodes being significantly longer.

Table 3.3: Mixed linear model results for post-drought episode length, df= 1454

| | **t value** | **p value** |
|---|---|---|
| Close Neighbour (any) | 0.57 | 0.56 |
| Female Neighbour | 0.57 | 0.56 |
| Male Neighbour | 0.60 | 0.54 |
| Calf Neighbour | 0.46 | 0.64 |

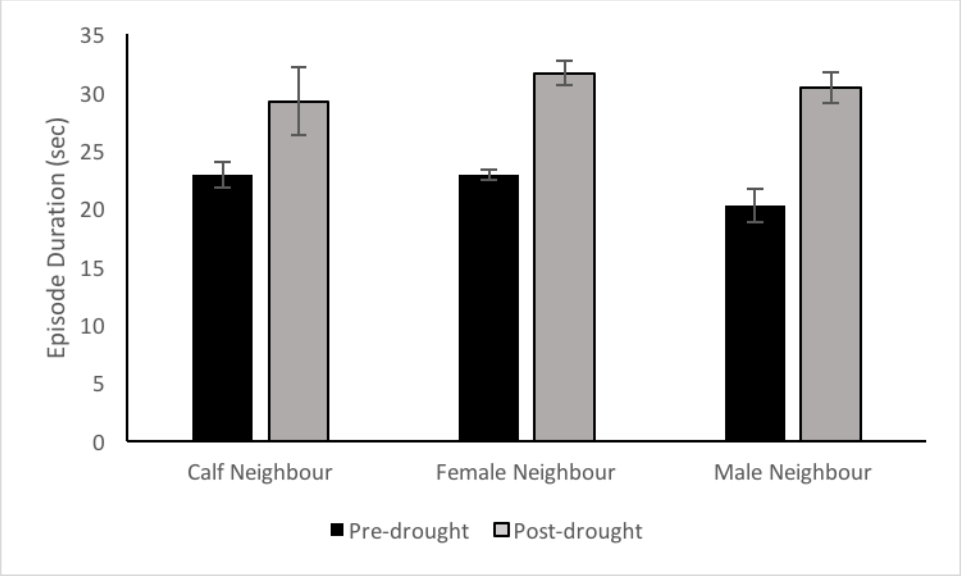


Figure 3.1: Average episode lengths pre- and post-drought for different neighbour type

## *Foraging Efficiency*

The mean bite per second for post-drought data, was 0.28 seconds, and there were no significant effects with any of the variables (Table 3.4). There were non-significant increases in efficiency for female giraffe with male neighbours. Female giraffe have become more

efficient with a male neighbour when compared to a female neighbour (Figure 3.2). While not significant, female giraffe became less efficient with a calf as their close neighbour.

Table 3.4: Mixed linear model results for post-drought foraging efficiency, df = 1886

| | **t value** | **p value** |
|---|---|---|
| Close Neighbour (any) | 0.35 | 0.72 |
| Female Neighbour | 0.25 | 0.79 |
| Male Neighbour | 0.42 | 0.67 |
| Calf Neighbour | 0.02 | 0.97 |

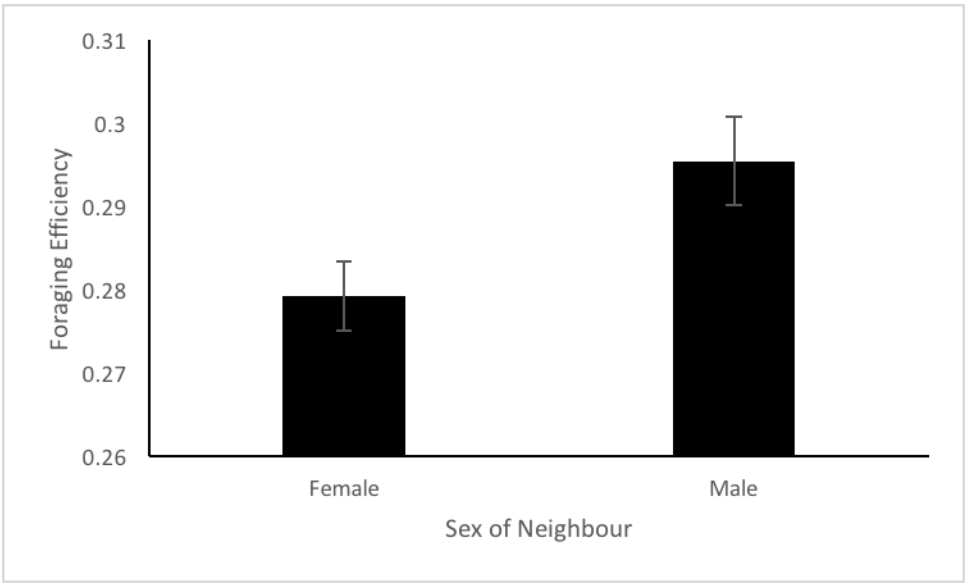


Figure 3.2: Post-drought foraging efficiency for female giraffe with a male vs female neighbour

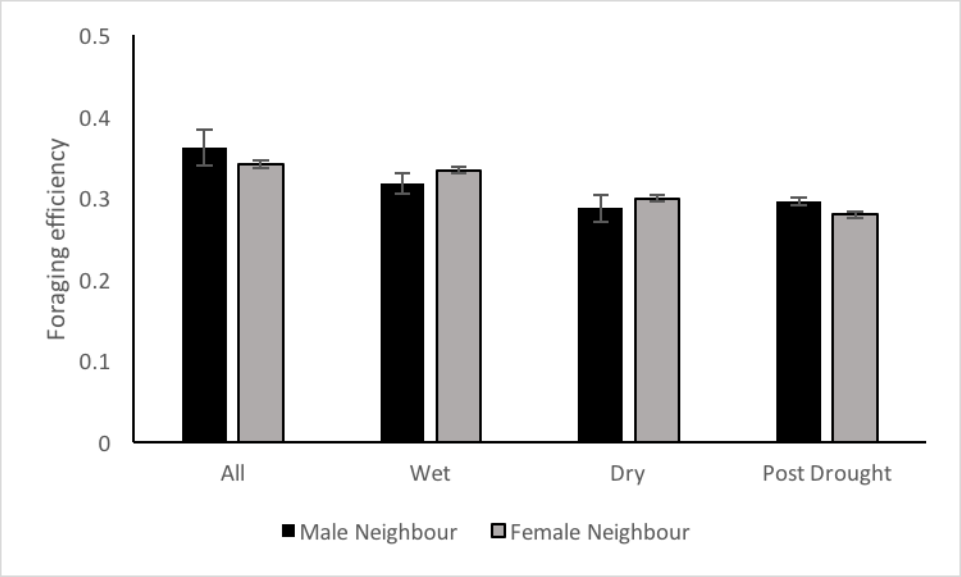


Figure 3.3: Comparison of all foraging efficiency data over all periods for female giraffe with a male vs female neighbour

*Foraging Efficiency including scans*

The mean bite per second for post drought data was 0.24 seconds. Again, there were no significant effects for any of the variables (Table 3.5). As seen with foraging efficiency, female giraffe are however slightly more efficient with a male neighbour compared with a female neighbour (Figure 3.4). This contrasts with the effects seen pre-drought (Figure 3.5).

Table 3.5: Post-drought mixed linear model results for foraging efficiency with scans, df = 1863

| | **t value** | **p value** |
|---|---|---|
| Close Neighbour (any) | 0.21 | 0.82 |
| Female Neighbour | 0.12 | 0.90 |
| Male Neighbour | 0.05 | 0.96 |
| Calf Neighbour | 0.37 | 0.72 |

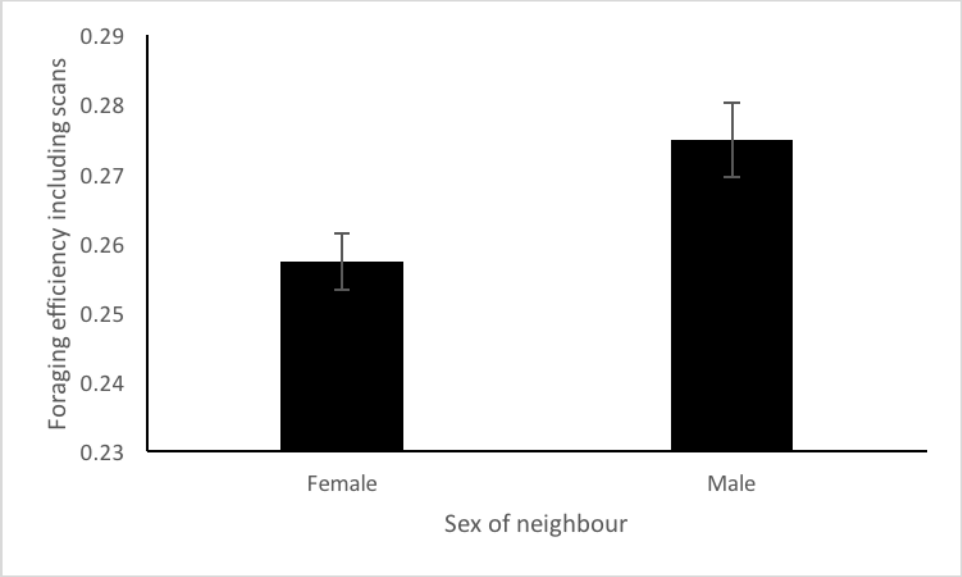


Figure 3.4: Post-drought foraging efficiency including scans for female giraffe with a male vs female close neighbour

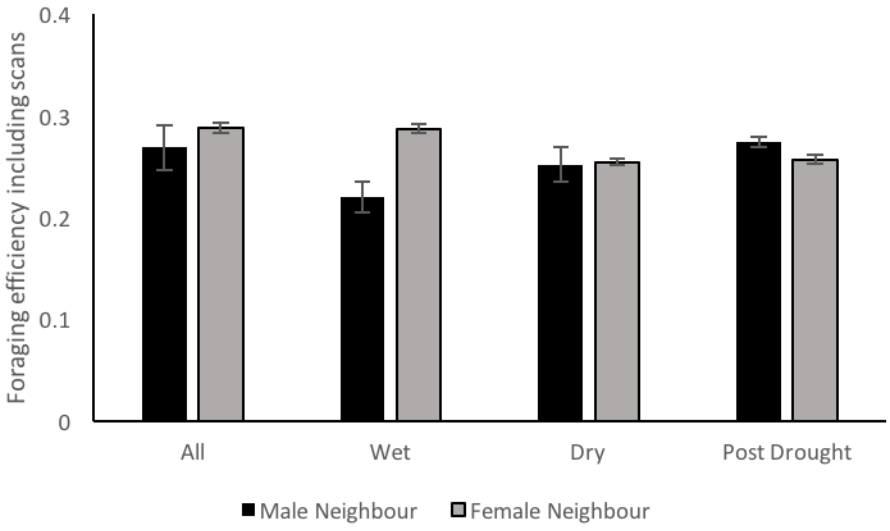


Figure 3.5: Comparison of all foraging efficiency with scans data over all periods for female giraffe with a male vs female neighbour

*Proportion time cost of vigilance*

Vigilance increased foraging time by 11% post-drought. There were no significant effects for any of the variables (Table 3.6). Proportion costs are highest in the pre-drought wet season and lowest post-drought (Figure 3.6).

Table 3.6: Post-drought liner model results for proportion time cost, df = 1813

| | **t value** | **p value** |
|---|---|---|
| Close Neighbour (any) | 1.14 | 0.25 |
| Female Neighbour | 0.80 | 0.42 |
| Male Neighbour | 0.76 | 0.44 |
| Calf Neighbour | 0.89 | 0.36 |

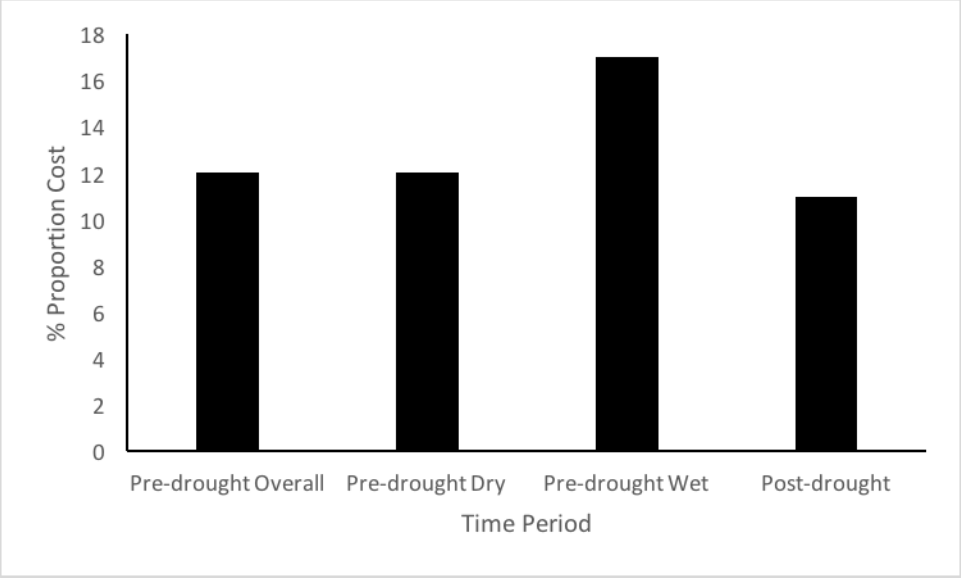


Figure 3.6: Comparison of percentage proportion cost for all collection periods

## *Discussion*

The average group size for giraffe does not change with season or environmental conditions. Similarly, the composition of giraffe groups shows little change by season, but did change in post-drought conditions. In dry periods male giraffe are more likely to be found in groups as opposed to solitary (Wolf et al., 2018), with male groups significantly larger post-drought. Males may not be adopting their roaming reproductive strategy as much in the dryer times so group with other males more if fewer females are reproductive (Wolf et al., 2018). This could then mean that males become less of a threat to females in terms of harassment in dry conditions such as drought.

Giraffe foraged for longer periods in the post-drought period compared to pre-drought. Giraffe were staying at a foraging patch for longer, potentially because there were fewer options for them to change trees. With the drought and reduction of food it becomes harder to find food. It could possibly be better to stay at less productive tree than walk away to try and find a different option. The length of the episodes is still longer with female neighbours compared to male neighbours, which means a female still forages for longer when her neighbour is another female.

Foraging efficiency in the post-drought late dry season was less than both the overall efficiency and wet season efficiency. With less food available, individuals become less efficient. Food could also be harder to access and may not as good quality, making it less appealing to the individuals and making them less enthusiastic and efficient (Owen-Smith, 2008). How giraffe feed may also contribute to a differing efficiency. When a giraffe feeds, it uses it's tongue to strip all the leaves off a branch (Parker, 2004). If there are less leaves on a branch it will take more effort to get more leaves per bite. There was no significant difference in foraging efficiency for female giraffe with or without a close neighbour and no difference with different sexes as a close neighbour. There may also be an increase in competition for this limited resource, resulting in continued foraging even on non-preferred forage items. There is a slight decrease in efficiency with scans and giraffe are slightly more efficient with a close neighbour present. Under strong competition, a close neighbour may

force an individual to eat more efficiently to compete (Chuard et al., 2018; Uccheddu et al., 2015).

While the results were not significant, female giraffe forage more efficiently with male close neighbours compared with female neighbours. In pre-drought conditions females are less efficient with male neighbours, although in the late dry season there is no difference between male and female neighbours. In post-drought dry season there is a greater tolerance for males as they are now more efficient with them present. Foraging competition may override the harassment avoidance benefits (Uccheddu et al., 2015). Furthermore, since males forage higher in the tree (du Toit, 1990), males may not directly be competing with females, as they could be foraging on branches that females can't reach. Males forage at higher heights during the dry season when forage is restricted (Kotze, 2007).

Female giraffe become less efficient at foraging after drought when their close neighbour is a calf. When vegetation was abundant in the wet season, female giraffe were most efficient when their calf was the closest neighbour. This implies that female giraffe may have become more protective by becoming more vigilant in drought conditions. With drought conditions and the resulting reduction in cover, the landscape becomes a lot more open which may mean females now have to be more wary and vigilant towards predators (Creel et al., 2005; Périquet et al., 2012). Female giraffe often keep calves to areas where there is ample cover to hide the calf, especially in the immediate period postpartum (Langman, 1977).

When there is less food available, female giraffe are less choosy about who is near them and have become more tolerant to the presence of male giraffe. There is no longer a significant difference in foraging efficiencies for any of our variables. There are also no significant differences in the proportion of foraging costs. This is consistent with the findings from the previous chapter that females were more tolerant in the late dry season, and the effect is slightly more exaggerated after the period of drought.

The need to obtain the required amount of daily food for survival may override the impulse of a female to move away from male. For giraffe, the predicted quantities of browse required daily are 50kg browse (that must provide 150 000 kj energy) for a mature 1000kg

giraffe (Mitchell et al., 2010). This is a large absolute quantity of leaves (which have low nutritional value) to obtain daily, requiring a large time commitment (du Toit & Yetman, 2005). Female giraffe may not have the energy to now worry about male giraffe close to them when not in oestrous or the potential threat of another female around her is in oestrous and may attract males. Alternatively, as a male giraffe is larger and requires more food, he may not have the time to invest to reproductive efforts.

There could be an increase in competition between individuals. As food has become a limiting factor they may now have to forage more efficiently to compete for the remaining food resources. When other individuals are in close proximity this may make individuals forage faster and more efficiently to outcompete the close neighbour for the food resource. Competition between individuals is most intense in the dry season (Simmons & Scheepers, 1996) and this will become more exaggerated in drought conditions which are more extreme than a normal dry season. When food is scarce during dry periods, female giraffe appear to spend more time with individuals that might be genetically related to them (Wolf et al., 2018). If there is less food there should be less competition if an individual is around kin (Silk, 2007).

In a drought period, there is a distinct change in vegetation meaning there are now less resources available for the animals in the area. Elephants will push down trees in times of drought to better access higher food resources (Bax & Sheldrick, 1963). With a reduction in resources, animals may divert what little they have away from other process, such as reproduction, and put everything into survival. Female giraffe can reabsorb or abort fetuses in times of drought (Mitchell et al., 2010). Lactation can cease and this causes unweaned calves that can't feed on anything else yet to die (Mitchell et al., 2010).

In a period of extended drought, female condition is reduced, such that many adult females are unable to breed until the drought ends (Mitchell et al., 2010). Drought in the study area officially ended in 2017 with good rainfall in the wet season commencing in October/November of that year. As a giraffe female is pregnant for 15 months, all the females in the area may already have been pregnant at the time of this study (August/September 2018). Therefore, if the females are already pregnant, the males no

longer pose a threat to their foraging as an already pregnant female won't be in oestrous and the males will not have to harass her to initiate mating.

This data reinforces what I previously found when looking at seasonal variation in Chapter 2. The dry season showed an increase in tolerance towards males and with the addition of drought on top of the late dry season, this effect is increased. The fission-fusion system of giraffe allows them the flexibility to be able to adjust their group size and composition to the changing food availability. With changes in the environmental conditions due to season and drought events, it is beneficial for giraffe to be able to adjust to the varying foraging situations.

## *Conclusion*

In conclusion, I found that females are more tolerant of males in dry/post-drought conditions. This could be due to a reduction in harassment behaviour from the males and changes in reproductive behaviour or that males use different food to females.
Their increased efficiency with close neighbours could be a result of increased competition due to lower food availability.

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# Chapter 4: Sexual segregation in a giraffe population in Kruger National Park; the effects of drought and limited resources.

## *Introduction*

Sexual segregation, where male and females of a species live in separate groups outside of breeding season, is found in a variety of species (Ruckstuhl, 2007). Sexual segregation is common in ungulates, particularly those with a polygynous mating strategy (Mramba et al., 2017), such as bighorn sheep (Ruckstuhl, 1998) and also seen in marsupials, (eg: the western grey kangaroo (MacFarlane & Coulson, 2007), and elephants (Siyaya, 2015). Generally, sexual segregation increases with body size dimorphism (Mysterud, 2000), with differences in body size leading to sexual differences in ecology and behaviour, possibly making it difficult for the two sexes to stay in the same group (Ruckstuhl, 2007). Segregation may be females avoiding the risk associated with male harassment by occupying different habitats (Darden & Croft, 2008). Females may also segregate due to vulnerability to predation of their young (Bleich et al., 1997). Thus, while the cause of sexual segregation is unknown, several factors related to dimorphism are implicated, such as social factors and ecological requirements, and the primary driver of segregation may be a combination of these factors (Loe et al., 2006).

There are several different hypotheses to explain the occurrence of sexual segregation. The four main hypotheses are outlined in Table One. The Predation Risk hypothesis predicts that anti-predator behaviour shapes segregation since females with offspring are more vulnerable to predation than adult males (Bleich et al., 1997; Bowyer, 1984; Main et al., 1996). Therefore, females with calves will use habitats that are safer from predators at the expense of forage quality while males will use habitats with higher predation risk but with better quality food (Ruckstuhl & Neuhaus, 2002). This would mean that females segregate themselves from males prior to calving and should be more pronounced amongst mothers with offspring (Loe et al., 2006). Other hypotheses are more directly linked to differences in body size. The forage selection hypothesis (Geist, 1974; Clutton-Brock et al., 1982; Main et al., 1996; Ruckstuhl & Neuhaus, 2002) is based on the Jarman-Bell Principle, which relates habitat segregation to sex specific nutrition requirements due to differences in body size (Clutton-Brock et al., 1982). The Jarman-Bell principle, that an increase in ungulate body size is associated with an increase in dietary tolerance, is a key component throughout these studies (Bell, 1986, 1971; Demment & Van Soest, 1985; Geist, 1974; Jarman, 1974). Large

herbivores have the nutritional advantages of decreased mass-specific metabolic needs, and increased gut capacities, resulting in an increased dietary tolerance with increasing body size. Consequently, the smallest ungulates have to feed selectively on the highest quality food available, whereas larger species (who probably also prefer the higher quality food) accept more abundant food of lower quality due to their daily intake requirements. The principle should also apply to intraspecific interactions within species with marked size dimorphism. Essentially, the higher mass-specific nutritional demands of females, coupled with the demands of gestation and lactation should result in females selecting for diet quality (Demment & Van Soest, 1985; Du Toit, 1995; Illius & Gordon, 1992). Conversely, males have a requirement for higher ingestion rates due to their larger size, and their size also results in higher tolerance of variation in diet quality. Therefore, males may be forced to forage in less depleted areas obtain sufficient forage quantity, leading to competitive exclusion from some areas by more selective females who have consumed the higher quality plant parts. Indirect competition has been proposed as an explanation for sexual segregation in grazing species (Conradt et al., 1999, 2001). Sexual size dimorphism is however most pronounced in species at the upper end of the range (Loison et al., 1999). In African elephants, females select higher quality plant parts, whereas males are less selective, although segregation by foraging height didn't occur, suggesting a lack of intraspecific competition during the study (Stokke & du Toit, 2000, 2002).

The activity budget hypothesis (Ruckstuhl, 1998; Ruckstuhl & Neuhaus, 2002) and the related activity synchronization hypothesis (Conradt, 1998a; Conradt, 1998b; Conradt & Roper, 2000) are again related to sexual dimorphism between males and females and the fact the females may be less efficient than males in digestion. It states that females will compensate for their lower digestion efficiency by foraging for longer periods of time while males will spend more time ruminating (Ruckstuhl & Neuhaus, 2002). This differing time spent foraging or ruminating is predicted to cause their feeding patterns to be asynchronous meaning they will stay in different groups for foraging (Loe et al., 2006). The social preference hypothesis suggests it is behavioural differences between the sexes that facilitate segregation (Bon & Campan, 1996). It hypotheses that females may segregate themselves to avoid aggression from males and males may segregate to develop social skills relating to dominance and fighting (Main et al., 1996; Bon et al., 2001).

Table 4.1: Sexual Segregation Hypotheses, assumptions and predictions for this study

| Hypothesis | Assumptions | Predictions |
|---|---|---|
| Predation Risk | Females with offspring minimise predation risk in safe habitats. Males maximise food intake in high quality habitats. | Sexual segregation will be greatest when offspring are young and most vulnerable to predation. |
| Sexual dimorphism, forage selection | Male and females have different nutritional requirements due to size differences (Jarman-Bell Principle). | Females will inhabit areas with higher quality food.<br>More segregation in species with more dimorphism.<br>Segregation will differ with food availability. |
| Sexual Dimorphism, Activity Budget | Females are less efficient at digestion than males. Differences in activity budgets will make synchronisation difficult. | Female giraffe will spend more time foraging than males and this will create asynchronous behaviour between the two sexes. |
| Social Preferences | Behavioural differences and social preferences can cause segregation. Females try to avoid male aggression and males may seek other males for social training. | Harassment levels will decline with a limited food supply.<br>Female giraffe will have a higher tolerance for close male neighbours that might harass them. |

In 1998, Conradt proposed a definition and measure of the degree of social segregation. Social segregation is the association of males and females in separate group and can range from no segregation to full segregation where all members of a population are separate. When no segregation in present the number of males and females per group should follow a random distribution (Conradt, 1998). Full segregation results in all male and all female groups (Conradt, 1998). In 2007, Bonenfant et al. (2007) suggested alterations to this coefficient to improve its robustness and allowed inclusion of solitary individuals in the equation, which allows for easier significance testing.

Giraffe provide an opportunity to test several of these hypotheses simultaneously. There is distinct sexual segregation in giraffe populations. There is a high degree of sexual dimorphism (one of the highest of all land mammals) between male and female giraffe, in both height and weight. Male giraffe weigh approximately 1200kg and female giraffe weigh approximately 800kg (Dagg & Foster, 1976). Males are also taller than females, with males ranging from 4.7m to 5.3m and females ranging from 3.9m to 4.5m (du Toit, 2001). Female giraffe are more likely than males to congregate in groups, especially with relatives, and males are more likely to be solitary (Carter er al., 2013).

Unlike most species, giraffe can exhibit sexually segregation on two different spatial scales (Ginnett & Demment, 1999). The first being on a habitat preference scale, with males preferring woodland habitats and females preferring more open areas (Young & Isbell, 1991). This segregation is a consequence of different reproductive strategies with females selecting areas suitable for raising offspring and males for maximizing body condition (Main & Coblentz, 1990). It may also be a result of male harassment and social influences from other giraffe (du Toit, 1990). This spatial segregation appears to not be driven by ecological factors such as foraging but potentially by social interactions.

The second scale is segregation within a habitat with different feeding heights (Du Toit, 1990; Young & Isbell, 1991). Males tend to feed on higher parts of trees while female giraffe tend to feed lower in the canopy (Mramba et al., 2017; O'Connor et al., 2015). Males may forage on the higher regions where no other animal can reach to feed more efficiently and gain more nutrients so they can spend more time on other activities, such as finding females or competing with rival males (du Toit, 1990). They are also much larger than females so they have a higher absolute energy requirement (du Toit, 1990). Males tend to spend more time feeding on a tree than females do, therefore allocating more of their foraging time to ingestion rather than moving between different forage patches (Ginnett & Demment, 1997). This sexual segregation in feeding is also believed to be related to the availability of nutrients found at the different levels of foraging heights (Mramba et al., 2017). The avoidance of tannins has also been proposed as a mechanism to drive this dietary segregation (Caister et al., 2003).

Season variation in resources could alter the degree of segregation in populations. The wet season sees a lot more food available with greater amounts of foliage present. The dry season sees a die-off of vegetation as it no longer receives enough water/rainfall to sustain the production of foliage. Vertical segregation in foraging height alters between areas with different resource availability (Mramba et al., 2017). The observed seasonal variation in giraffe group composition could also affect sexual segregation as different group configurations have also been recorded (Wolf et al., 2018). While giraffe are non-seasonal breeders and are asynchronous, there has been evidence in certain populations that there are more fertile females in the rainy season (Wolf et al., 2018). This could increase the chance of there being more groups observed that contain both males and females (less segregation) as males may be more inclined to roam and find receptive females in that period. It could however also mean that we are less likely to see males in groups as they are roaming around by themselves while looking for mates. Post-drought observations will investigate the effects of food limitation and lack of resources in the most extreme case. Knowing how these events affect giraffe behaviour can help us understand their ecology requirements in wake of sustained drought.

In this chapter, I aim to determine if sexual segregation in giraffe populations differs with food availability by comparing pre-and post-drought segregation data. I will examine if the sexual dimorphism hypothesis is contributing to segregation when food availability is altered during drought periods. I hypothesise that sexual segregation on a horizontal scale will be less pronounced during a drought as the decrease in food availability will cause all individuals to have to forage in closer proximity (Table 1). I will also consider if the social preference hypothesis does contribute to the observed segregation, by the means of females avoiding male harassment behaviour and segregating themselves (Table 1). I will test the activity budget hypothesis and see if synchronous behaviour in giraffe differs for different group types and if there is a difference in the occurrence of fission-fusion events. It is predicted that female giraffe will spend more time foraging so will create asynchronous behaviour that will result in greater segregation (Table 1). I will also look at the predation risk hypothesis and determine if there is a difference in segregation in female giraffe with and without calves present. It is predicted that females with calves will be more segregated than those with no offspring (Table 1).

## *Methods*

Giraffe groups were observed in Kruger National Park, South Africa over two distinct periods. The first was between July 2001 and July 2002 in the Tsokwane region, based at the ranger station (24o 47'S, 31o 52'E). This collection was made the two years following a large flood event in 2000. With large amounts of water present the previous year, the growth for the following seasons was high. Vegetation was plentiful and looked to be of a high quality. The second period of collection occurred in August and September 2018 (late dry season), in the region between Satara, Skukuza and Lower Sabie rest camps (inclusive of the Tsokwane region). Since the first collection, Kruger National Park has undergone a sustained period of drought over a two-year period from 2014 until 2016. According to the SANSParks official website, the wet season of 2014/2015 saw only 255mm fall which is only 65% of the yearly average. It became even worse the following year with the 2015/2016 season only having 190mm rain as opposed to the normal 550mm (52% of the normal average). The 2016/2017 season saw an increase in rainfall with 371mm falling. The 2018 dry season has been particularly hot and dry again with the onset of the rainy season not starting until November, a month later than normal. This drought has dramatically changed the vegetation cover and food availability in the park. The habitat was previously dominated by woody vegetation but post drought has become a more open grassland (Cameron, personal communication; Figure 1.4), aided in part by elephants knocking down trees at greater rates in times of drought (Bax & Sheldrick, 1963). Vegetation in the area is consisting of mixed woodlands, comprised mainly of acacia and marula species, and open savannah grasslands.

Giraffe were located opportunistically while driving public roads during daylight hours. Routes were varied daily so the same roads were not driven at the same time each day. Observations were made from inside a vehicle due to safety regulations of Kruger National Park. Giraffe are habituated to the presence of vehicles due to the large number of tourist vehicles they encounter, therefore the effect our presence while observing would be minimal.

Once giraffe were located, group composition and size was recorded for every giraffe encountered, with all individuals within 100m of each other considered to be members of the group (van der Jeugd & Prins, 2000). There are problems with defining a group that may

be relevant to giraffe as human observers may lack the ability to measure a group as perceived by a giraffe (Cameron & du Toit, 2005). Giraffe could exist in large dispersed wide ranging social groups due to their increased range of vision and other potential methods of communication (Doherty, 2005). However, this should not affect our ability to gain an accurate segregation measure. Age group (adult, sub-adult, juvenile or calf) and sex was recorded for all individuals. Individual activity was recorded each member of the group (what each individual was doing throughout the observation period). Fission-fusion events were also recorded. This was defined as an individual leaving or joining the current group.

*Data analysis*

Composition data was used to calculate social sexual segregation index using the segregation coefficient (SC) proposed by Larissa Conradt (1998). The resulting 'degree of segregation' ranges from 0 (where there is no segregation) to 1 (where all males and females segregate) (Conradt, 1998).

$$SC = 1 - \{(N / X.Y) \sum (XiYi / Ni - 1)\}$$

This coefficient has since been modified to a sexual segregation and aggregation statistic (SSAS) (Bonenfant et al., 2007). This modified index has the benefit of including solitary animals. This was also calculated for all data.

$$SSAS = 1 - \{N / (X . Y) \sum (XiYi / Ni)\}$$

These coefficients allow for a comparison of segregation within the Kruger population pre- and post-drought as well as examining seasonal variation within the pre-drought collection.

Chi-squared tests were performed for synchronisation and fission-fusion data to determine any significant differences.

## *Results*

During 2001 and 2002 (including both wet and dry seasons), 455 groups were encountered, with a total of 1639 giraffe. In 2018 observations were carried out over 22 days in the late dry period with 162 giraffe groups encountered, with a total 758 giraffe.
Pre-drought data had an average group size of 4.97 while post-drought data has an average group size of 4.67.

## Segregation Index

Segregation index was calculated to test if there is a difference in segregation with varying food availability to test the sexual dimorphism/foraging selection hypothesis. It is predicted that males and females will inhibit different areas to gain their required nutritional intake and this may change with seasonal variation and extreme changes in food availability (Table 4.1).

### *Segregation Coefficient*

Overall the whole period between July 2001 and July 2002 the social segregation index was 0.210. This was then broken down into seasonal variation. During the wet season the segregation index was 0.232 (Figure 4.1). During the dry season, the SC decreased to 0.197 (Figure 4.1). The 2018 data was collected in the late dry season and had a SC of 0.287 (Figure 4.1).

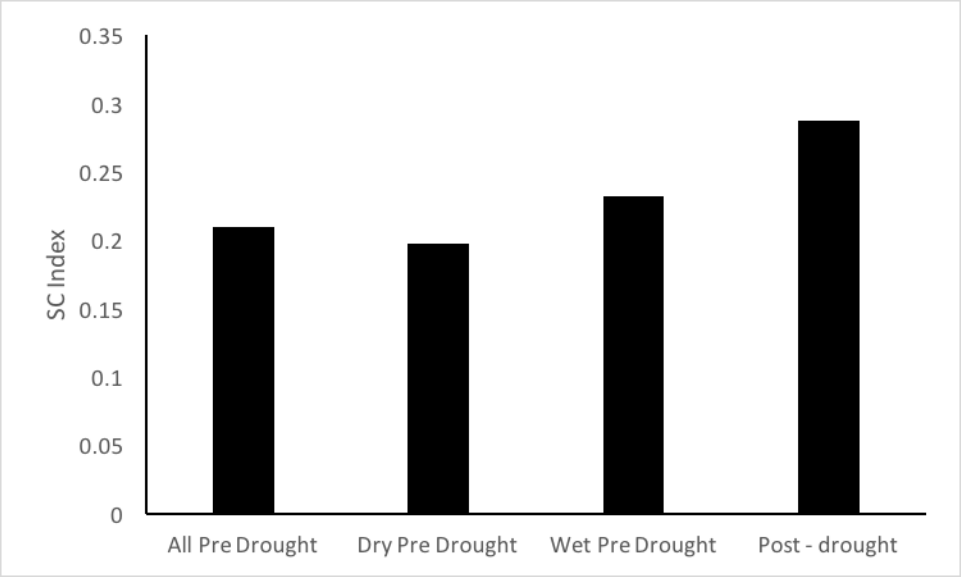


Figure 4.1: Sexual Segregation Index (SC) for all data periods

The sexual segregation coefficient has shown that giraffe have become 7% more segregated overall after a sustained drought period. Between the initial dry season and the post drought dry season there has been a 9% increase in the sexual segregation coefficient.

*Sexual Segregation Aggregation Statistic*

Using the sexual segregation and aggregation statistic (SSAS), the overall pre-drought period had a coefficient of 0.488. When looking at the different seasons, the wet season was 0.388 and the dry season was 0.357 (Figure 4.2). The post-drought data had a coefficient of 0.521 (Figure 4.2).

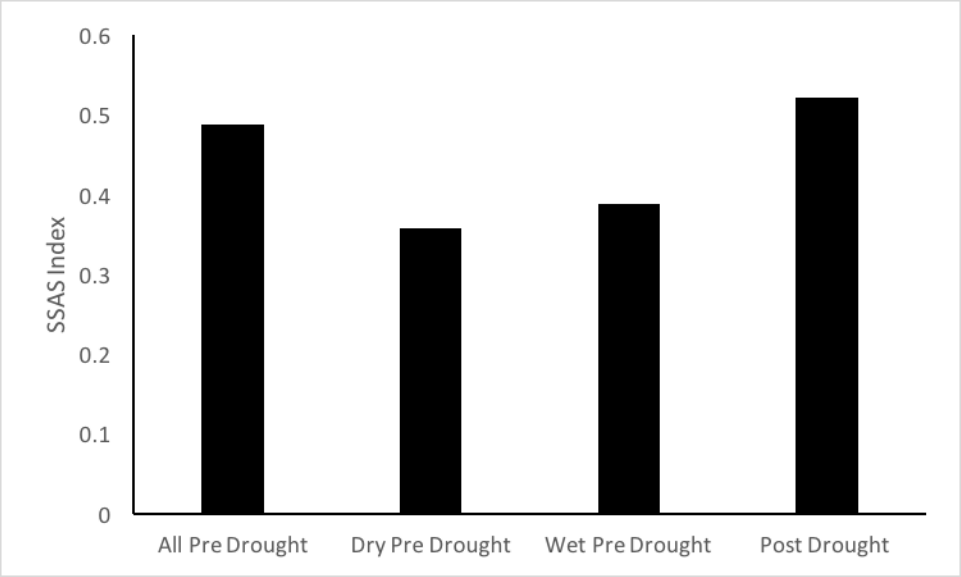


Figure 4.2: Sexual segregation and aggregation statistic (SSAS) for all data periods

Using the SSAS, there was an overall increase of 3% between the pre-and post-drought data. This is less of an increase than seen with the SC. When comparing the dry season data, we saw an increase of 17%, which is a substantial increase when compared to the SC.

While the values differ between the two coefficients the general trends are the same. There is an increase in the overall segregation between pre- and post-drought data. There is also a considerable increase in segregation between the two dry seasons. Seasonal variation within the first data collection period, with good food availability, shows that giraffe become less segregated in the dry season.

## Female with calves

Both sexual segregation indexes (SC and SSAS) were calculated for female giraffe with and without calves present, for the pre-drought and post-drought data. This will investigate if female giraffe are segregating more or less with calves and determine if the predation risk hypothesis is supported.

Table 4.2: Sexual segregation measures for female giraffe with and without calves present, comparing pre- and post-drought conditions.

| | Pre-drought | Post-drought |
|---|---|---|
| Calves SC | 0.003 | 0.02 |
| Calves SSAS | 0.186 | 0.26 |
| No Calves SC | 0.06 | 0.107 |
| No Calves SSAS | 0.25 | 0.316 |

## Synchronisation

Individual activity was recorded and compared to other members of the groups to determine if groups members were synchronous in their behaviour. This will determine if the activity budget hypothesis is causing giraffe to segregate.

Table 4.3: Number of groups with 80% synchronous behaviour or mixed activities.

| Group Type | Synchronous | Mixed Activities |
|---|---|---|
| Mixed Sex | 114 | 71 |
| Males Only | 16 | 0 |
| Females only | 106 | 0 |

Table 4.4: Number of groups with 95% synchronous behaviour or mixed activities.

| Group Type | Synchronous | Mixed Activities |
|---|---|---|
| Mixed Sex | 86 | 99 |
| Males Only | 16 | 0 |
| Females only | 103 | 3 |

There is a significant difference with 95% synchrony, (chi squared = 70.42, p = <0.001). Mixed groups have less synchronous behaviour than single sex groups.

## Fission-fusion events

Fission fusion events (giraffe leaving or joining) were recorded for groups encountered. This will indicate if giraffe are segregating themselves due to asynchronous behaviours.

*Fission events*

Table 4.5: Number of groups that had a fission event as opposed to groups with no changes in composition

| Group Type | Fission event | No change |
|---|---|---|
| Mixed Sex | 8 | 102 |
| Males Only | 1 | 17 |
| Females only | 1 | 98 |

There is no significant difference between group type for fission events (chi-squared = 5.03, 2 df, p=0.08).

*Fission and fusion events*

Table 4.6: Number of groups that had a fission or fusion event as opposed to no changes in composition.

| Group Type | Fission or fusion events | No change |
|---|---|---|
| Mixed Sex | 15 | 95 |
| Males Only | 2 | 16 |
| Females only | 2 | 97 |

There is a significant difference in fission fusion events (chi-squared = 10.56, 2df, p=0.005). Mixed groups have the most changes (14%) followed by all male groups (11%). Female groups showed low levels of change (2%). Note: there were very few all male groups observed.

## *Discussion*

The pre-drought data for the dry season supports my original hypothesis that giraffe will become less segregated when there is less food available. With fewer resources available in the late dry season, there will be fewer foraging options and giraffe are more likely to be found together to use the remaining food sources. Other studies also show that giraffe group more in the dry (Wolf et al., 2018) and this is supported by our data. Males and females will join in these groups out of necessity to gain foraging opportunities.

In the wet season, we saw slightly more segregation. This is supported by recent research, where males were more likely to be solitary in the wet season (and therefore segregated) as they might spend more time roaming between different female groups searching for receptive females (Wolf et al., 2018). Female giraffe tend to associate with other females more in the wet season, again potentially increasing the segregation seen (Wolf et al., 2018). This fits with the social preference hypothesis, if females are segregating themselves more to avoid the harassment from males looking for mates. Chapters 2 and 3 showed that females are less tolerant of male close neighbours in the wet season. If they are less tolerant they may leave the area if males are present, therefore segregating themselves. As food is readily available they should be able to find another food source easily.

Giraffe are segregating slightly more post-drought than there were before the drought. This becomes even more pronounced when looking at the two different dry season values. With less food available it can become more difficult for individuals to find the right food that is necessary to meet their nutritional requirements. Giraffe could now need to be more separated spatially to ensure that they are able to get the required food from different sources to ensure survival. If they are more segregated, there are more foraging opportunities for individuals and less competition for the few trees remaining. This supports the sexual dimorphism/forage selection hypothesis. The need to find different types of forage is driving giraffe to inhabit different areas and therefore become more segregated. This has been seen with smaller herd sizes in the dry season (Bercovitch & Berry, 2010). Conversely, Wolf et al. (2018) found that herd size seemed to increase in the dry season.

Those groups however tended to be multi-female or multi-male groups as opposed to mixed sex groups, which could still fit with an increase in segregation.

By segregating more in drought conditions, competition between individuals is reduced meaning that giraffe will have a better chance of gaining the required food quantity and quality needed for survival. A mature giraffe requires an estimate of 50kg of browse daily (Mitchell et al., 2010). To ensure that this is reached it would be beneficial for a giraffe to have less competition from other giraffe for the limited amount of browse still available during a drought.

As males and females also segregate on the vertical scale (Ginnett & Demment, 1997), males may now have to be further away from females to be able to find more food at their preferred height. There is indirect feeding competition between male and female giraffe, and this creates vertical segregation in foraging (Kotze, 2007), and may also be influencing the horizontal segregation. Kotze (2007) showed that vertical segregation increased in the dry season. Males benefit from foraging higher on the tree to take advantage of the nutrient rich new shoots (du Toit, 1990). The trees available post-drought on which females can still browse on may be insufficient for males to obtain the required bulk of food, so they need to find trees elsewhere to meet their requirements. The need to find different trees may force these giraffe to move to different habitats, increasing segregation. Further investigation into how vertical segregation is affected would be beneficial to increase understanding of these seasonal changes.

There are low levels of segregation pre-drought for female giraffe with calves present. This indicates that females are not selecting safer habitats, which does not support the predation risk hypothesis. Post-drought, we see that female giraffe are segregating less when they have a calf present. It could be with the post-drought reduction in vegetation there is a distinct lack cover that a female giraffe would normally favour with a new calf (Langman, 1977). If there are now no longer the options and habitat differences, females may no longer segregate themselves. Males may also be seeking out groups with young calves due to females starting to cycle again now they have given birth (Mitchell et al.,

2010). If males are seen staying around these females this would increase the number of multi-sex groups and decrease the amount of sexual segregation.

Analysis of synchrony in giraffe groups show that mixed sex groups have less synchronised behaviour than same sex groups. Same sex groups have a large proportion of synchronicity meaning that when giraffe were with members of the same sex then they are likely to be doing the same activity (i.e.: feeding). If a group is less synchronised it will be more likely that they will end up separating as they engage in different activities (Ruckstuhl & Neuhaus, 2002).

Fission-fusion events show that in mixed sex groups there are a significant amount of changes occurring within the group. Individuals leave and join groups at a higher rate than in single sex groups. The lowest amount of changes occurs in all female groups while male groups are slightly higher. These results are similar to, and support, recent research by Castle (2018), who also found that male have a higher rate of fission-fusion events than females and that mixed groups have the highest rates of fission-fusion events. These results also support the activity budget hypothesis, with mixed groups with both sexes not being synchronised and more fission-fusion events occurring as individuals segregate.

## *Conclusion*

In dry seasons, there is less segregation in giraffe populations. This fits with a reduction in food causing fewer foraging options which forces individuals to forage in closer proximity to use the remaining resources. After a period of sustained drought, I found that giraffe segregate more than all other time periods. This could be due to the extent of foraging loss, causing individuals to disperse further and inhabit different areas to be able to find food that meets their nutritional requirements. This could also be driven by competition between individuals for the remaining limited resources.

I found support for three of the four main sexual segregation hypotheses that are based on differences in body size. The forage selection, activity budget and social preference hypotheses can all be seen to contribute to the observed sexual segregation in this giraffe population. These hypotheses are all related to differences in body size creating circumstances that make separating from the opposite sex advantageous. However, I found no evidence to support the predation risk hypothesis, as females are not segregating more with calves, and post-drought are segregating less.

Sexual segregation is more than likely caused by not just one factor but an interaction of several different factors. Several hypotheses for sexual segregation can play a part in determining the degree and type of segregation in a population.

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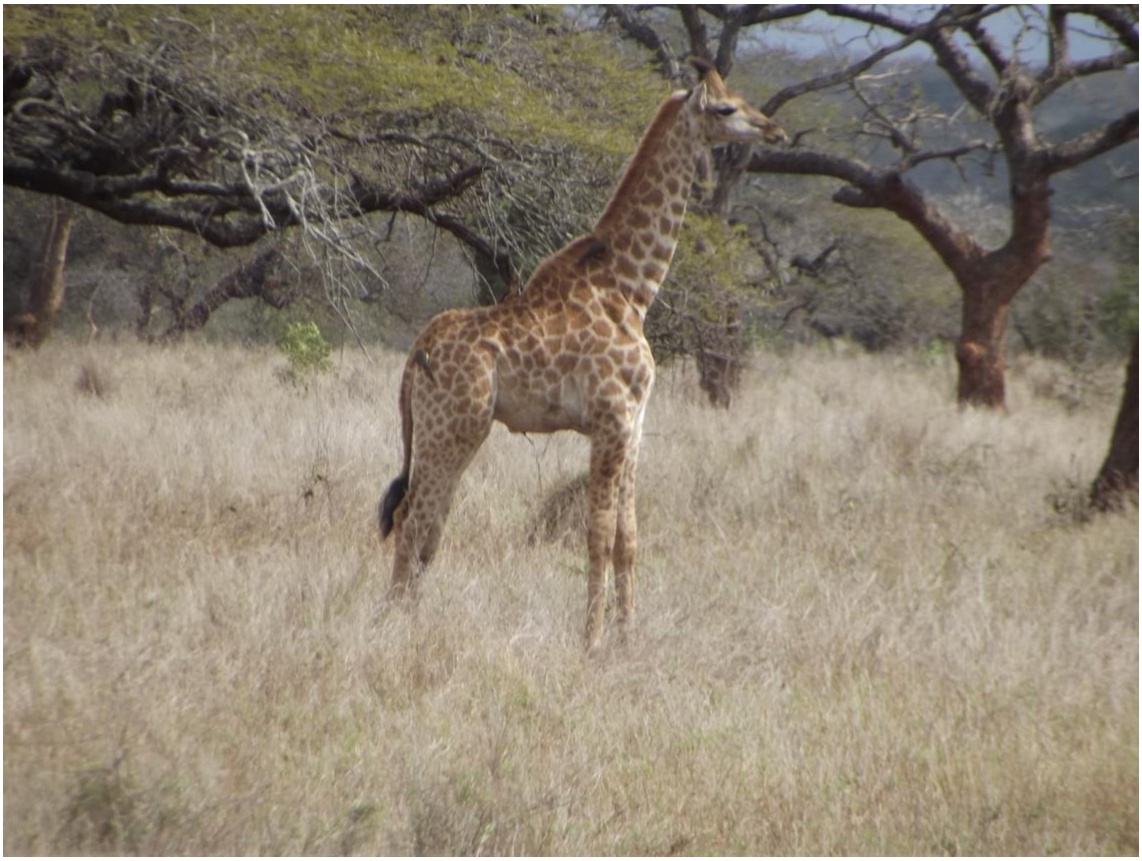
# Chapter 5: Thesis General Discussion



I have shown that giraffe were influenced by their close neighbours and that this may have more of an influence on their behaviour than the composition of the entire group. With a fission-fusion dynamic, the social interactions within a group are fluid and the behaviours that govern the formation and movements within these groupings is poorly understood (Kasozi & Montgomery, 2018). With no permanent bonds, the identity of close neighbour may influence individuals more than in other social groupings. By understanding how an individual's neighbouring conspecific affects their behaviour this can help to give a better understanding of how the social structure is maintained. It also reduces the need to define an arbitrary group for a species where it is difficult to assess.

The effect that a conspecific has is dependant in part on the season and the food availability in an area. When food is plentiful close neighbours effect individual giraffe, as giraffe cows are less efficient at foraging when a close neighbour is present, specifically when her close neighbour is a male. A female is less tolerant to the presence of a male conspecific and does not forage as efficiently as she could (Chapter 2). However, when food becomes a limiting factor, giraffe seem to be more tolerant to the presence of a conspecific (Chapter 3). Less food availability sees no change in the foraging efficiency of giraffe with or without a close neighbour, which could mean they are no longer as concerned about the proximity of neighbours. This helps to support the idea that fission–fusion dynamics are a product of ecological variation (Webber & Vander Wal, 2018). In the dry season, there are fewer food options as the lack of rain hinders growth and causes plants to die. It has been seen that in this dry season giraffe have smaller herd sizes (Bercovitch & Berry, 2010). This shows how the flexibility of a fission-fusion society can be beneficial as smaller groups will mean that there is less competition for the limited resources.

The reproductive status of a female may influence close neighbour effects. Female giraffe may be more fertile and receptive in the wet season (Wolf et al., 2018) then the harassment risk presented by males becomes greater. If the threat of harassment is higher than a female may be more likely to become more vigilant when a male is around and therefore forage less efficiently (Cameron & du Toit, 2005).

In the dry season, there is less segregation as there are fewer foraging options. However, there may still be sufficient food to allow males and females to continue to browse off the same trees. With less foraging options individuals are more likely to be foraging closer to others as it may be difficult to find alternative forage. After the occurrence of drought, the forging loss becomes more extreme. The trees that could once sustain both sexes may now no longer have the required nutritional value and individuals (more than likely males) may have to look elsewhere to find food that will be sufficient to maintain them. This supports the forage selection hypothesis for sexual segregation (Ruckstuhl & Neuhaus, 2002). The varying food availability in the different seasons will create segregation due to the varying food requirements for the different sexes.

Sexual segregation is hypothesised to be influenced by the social preference of individuals (Bon & Campan, 1996). This is consistent with the results found in this thesis. Chapters 2 and 3 have shown that behaviour can influence the social structure of individuals while foraging and this can then affect the segregation. If a female does not want to be around a male to avoid his aggressive behaviour (Bon et al., 2001), they will leave the area where a male is, increasing the segregation. Differences in body size and the differing forage requirements are also important factors influencing sexual segregation in giraffe populations (Chapter 4), especially when extreme food loss is observed in times of drought. Sexual selection therefore may not be created by just one hypothesis but a mixture of several factors.

It is important to have knowledge of environmental conditions as seasonal differences can have large effects on giraffe behaviour. Giraffe forging behaviour is influences by food availability which is season dependant. Less food is available in dry seasons while it is plentiful during the wet season. The food availability will determine how many giraffe are present at a location and can help predict where they might move to find alternative food sources. Knowing the conditions an area encounters can help to predict giraffe behaviour. By knowing the predicted movements of a population of concern, we can help predict the potential mating and reproductive success, which ultimately will determine the population's survival.

Social influences can affect many aspects of giraffe ecology, from foraging and habitat selection to mating success and reproduction. My thesis has helped to improve knowledge on a small part of the puzzle, how social interactions of giraffe can affect their foraging success and how those interactions can contribute to sexual segregation. There are still more avenues to investigate to help complete the big picture of giraffe behaviour and ecology. Food limitation impacts the social interactions in giraffe populations and knowledge of environmental conditions that can alter food availability is important for conservation efforts for this species. By looking at close neighbour effects in a fission-fusion species we can better understand the costs and benefits of grouping and how these groups are formed and maintained.

*Importance*

A better understanding of giraffe ecology and biology is important in the face of population declines currently being witnessed in many areas in Africa. With increased knowledge, we can make better informed management plans and help the species continued survival. Social behaviours are important to understand especially in terms of the fission-fusion dynamic as translocations are becoming an important tool for conservation work. By knowing how giraffe interact and the dynamics within a group, we can help to increase chances of a successful translocation (Castles, 2018). These social interactions can affect the mating success within a population and that ultimately affects the population survival. Knowing the environmental conditions and changes in food availability that an area undergoes can help to decide the number of animals as well as the individuals that can be moved to the new location.

An increased knowledge of behaviour and social interactions and structure can also help to improve conditions in captive populations (Castles, 2018), by helping keepers with their daily husbandry as well as helping animal managers and species coordinators with grouping decisions and transfers between facilities.

## Future directions

*Communication*

Recently it has been noted how little research has been conducted on giraffe and how more research is required to help better understand this prominent species (Kasozi & Montgomery, 2018; Muller et al., 2018; Wolf et al., 2018). It is important to continue to expand our knowledge on this vulnerable species to be able to make better management decisions and help to stem the loss of individuals.

Giraffe communication is an important and understudied aspect of giraffe ecology. As we as humans lack the ability to measure a group as perceived by a giraffe, what we consider to be a group may have little relevance to a giraffe (Cameron & du Toit, 2005). The use of infrasound and olfactory cues and the fact they have a greater distance of vision means that to be able to have cohesion in a group, they could exist in large dispersed wide ranging but relatively stable social groups (Doherty, 2005). Understanding methods of communication can help articulate the processes by which they locate one another as part of their fission-fusion social structure (Kasozi & Montgomery, 2018).

Several studies have tried to establish what the mechanisms are that giraffe use to communicate. Visual, auditory and olfactory methods have all been presented as methods employed by giraffe (Kasozi & Montgomery, 2018). Only 21 studies have been conducted on giraffe communication over a 60 year period (Kasozi & Montgomery, 2018).

Auditory communication such as snorts, hisses, hums, bursts and growls have all been identified as signals used by giraffe (Kasozi & Montgomery, 2018). Infra sound has been proposed as a means of auditory communication (Bashaw, 2003; Von Muggenthaler, 2013) but other research has found no evidence of this (Baotic et al., 2015). Baotic et al. (2015) however found and recorded other vocalisations, including a ‘nocturnal hum’. It may be that giraffe employ both infrasonic and audible noises in their communication, but there are too few studies to be able to make a definite conclusion (Kasozi & Montgomery, 2018).

Olfactory communication has also been proposed to occur in giraffe populations. Olfaction is important in other social systems, for example individual recognition in sheep (Kendrick, 1994) and in sexual attraction and inducing ovulation in female goats and sheep (Delgadillo et al., 2009). However very little research has been conducted to determine if this is the case in giraffe. It has been found that giraffe have a distinct odour that could be used to distinguish individuals (Wood & Weldon, 2002). It has also been found that giraffe are capable of discriminating between different scents (Pereira, 2013). Communication by scent, however, is still not understood.

Giraffe have been found to have acute vision (Mitchell et al., 2013; Veilleux & Kirk, 2014). Their height allows for a longer range of vision which could mean group members can be at a greater distance from individuals than we are able to perceive as being members of the group (Doherty, 2005). However, it has not been investigated how vision is used for communication purposes, or whether it is used in maintenance of group integrity over large distances.

There is still a need to further study communication to better understand social structure (Kasozi & Montgomery, 2018). By better understanding communication it can help us better understand the giraffe fission fusion social structure. It will help us understand how groups are formed, kept together and how they interact (Kasozi & Montgomery, 2018).

*Vertical segregation*

I have shown that there is an increase in horizontal segregation in giraffe populations in time of reduced food availability and drought. Further research could test if these conditions also increase the vertical segregation within a giraffe group. This would help us to confirm if vertical segregation, in terms of nutritional differences in remaining forage, is also driving the observed horizontal segregation. It would also be interesting to know if a decrease in foraging options is forcing individuals to forage on suboptimal food at different heights as options are limited.

## *Conclusion*

In conclusion, we have found that there is an effect of a giraffe's close neighbour on their behaviour and this alters their foraging efficiency. It has emphasised how important social behaviour is in understanding the ecology of species and can help influence conservation efforts. It had also highlighted the importance of knowing the environmental conditions as these also play a role in determining these behaviours.

It has also been noted that giraffe behaviour is still under studied and would benefit with more research to help expand our knowledge to help protect this now vulnerable species.

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# Appendices

## Appendix 1: New Zealand Animal Ethics Approval

UNIVERSITY OF CANTERBURY
Te Whare Wānanga o Waitaha
CHRISTCHURCH NEW ZEALAND

ANIMAL ETHICS COMMITTEE

Secretary, Rebecca Robinson
Email: animal-ethics@canterbury.ac.nz

7th August 2018

Ref: AEC Application 2018/08R

Natasha Sutton
School of Biological Sciences
UNIVERSITY OF CANTERBURY

Dear Natasha,

Although the AEC cannot officially approve any application that occurs outside of New Zealand jurisdiction, the Committee felt your project met the ethical standards to proceed.

Thank you for submitting your application for assessment by the AEC, and we hope your project proceeds successfully.

Yours sincerely

James Briskie

Professor Jim Briskie
***Chair***
***University of Canterbury Animal Ethics Committee***

Appendix 2: South African national parks research permit

**ISSUE DATE** 02 August 2018

To develop, expand, manage and promote a system of sustainable national parks that represent biodiversity and heritage assets, through innovation and best practice for the just and equitable benefit of current and future generations.

South African NATIONAL PARKS

**Research Permit: Kruger National Park**
**REFERENCE:** SUTN1535

**Scientific Services**
**Kruger National Park, Private Bag X402, Skukuza, 1350**

| | |
|---|---|
| Sutton N | The Silent Extinction: Do social interactions limit giraffe foraging efficiency and contribute to giraffe population declines? |
| Co-Workers | Cameron E.Z. |

addo elephant
agulhas
augrabies
bontebok
camdeboo
golden gate highlands
karoo
kglalagadi transfrontier
knysna lake area
kruger
mapungubwe
marakele
mokala
mountain zebra
namaqua
table mountain
tankwa karoo
tsitsikamma
richtersveld
west coast
wilderness

**Herewith the permit for your research project valid from 01 January 2018 until 31 December 2018. The approval is subject to the following conditions. The Park Management staff must be contacted prior to entry into the park (see website for contact details).**

**Standard Conditions:**
PLEASE CONTACT THE PARK MANAGEMENT STAFF IF RESTRICTED AREAS NEED TO BE ACCESSED.
No damage shall be permitted to any natural vegetation, environment or property.
Uncontrolled vehicle access and parking could cause damage to vegetation and soil erosion and therefore only the use of approved vehicles routes and parking areas is allowed.
Fires can cause loss of vegetation, soil erosion and life and therefore fires, and braai's are not permitted unless in dedicated braai areas.
Other visitors to the area and or neighbours may not be hindered in any way.
No pollution or excessive noise is permitted.
Your permit must be retained and kept on your person at all times, and produced on request.

The areas under the control of SANParks are used entirely at your own risk. South African National Parks, its Board, directors, employees and agents are not liable for any loss or damage to the property or possession of any guest or participant (or accompanying minor) whether such damage is caused by the negligent act or omission of South African National Parks; arising from death or any bodily injuries of whatsoever nature sustained by a guest or participant (or accompanying minor) whether such injuries are caused by the negligent act or omission by South African National Parks, and/or by the defective functioning of any apparatus. The guest or participant and/or his/her/their estate hereby indemnifies South African National Parks against any claim, action, judgment, costs and/or expenses which may be made against South African National Parks and as may in any way be related to the above. The onus lies with the company or applicant to ensure that they are adequately insured.
Please note that you (your delegates, staff etc) are subject to the conditions set in terms of Section 86(1) of the National Environmental Management Act (107 of 1998) and the National Environmental Act: Protected Areas Act (Act 57 of 2003) for the duration of your stay in the National Park. Your attention is specifically drawn to sections 64(1) (a), (b) (c) which refers to penalties in terms of the Act.
SANParks staff's instructions, notices, regulations and signs must be complied with.
The activity shall be restricted to the area applied for.
Gate and operating times to be complied with.
NO PETS ALLOWED

**Special Conditions:**
**Any contraventions of the above will result in your permit being revoked**
SIgned on behalf of SANParks S.N Nabuza

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